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ON THE COVER: RECONSTRUCTION OF *AMBLYRHIZA INUNDATA*,
THE EXTINCT GIANT HEPTAXODONTID OF ANGUILLEA (DAN BRUCE,
1992; WITH PERMISSION OF THE ARTIST).

MACPHEE: HEPTAXODONTID BASICRANIA AND RELATIONSHIPS

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BASICRANIAL MORPHOLOGY AND
RELATIONSHIPS OF ANTILLEAN
HEPTAXODONTIDAE
(RODENTIA, CTENOHYSTRICA, CAVIOMORPHA)

R.D.E. MACPHEE



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CTENOHYSTRICA, CAVIOMORPHA)

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ABSTRACT

What, if much of anything, are “Antillean heptaxodontids”? Over the course of nearly a century and a half, these caviomorph rodents, with their distinctive quasilamellar cheek teeth and generally large body size, have been diversely regarded as members of Chinchilloidea, or Caviioidea, or Octodontoidea; as distinct enough to warrant their own family or subfamily, or as no more than an offshoot within Dinomyidae or Capromyidae; and as having diverged from other caviomorph clades as early as the Oligocene, or as recently as the late Neogene. Similar uncertainties concern the taxonomic content of the group. It has been repeatedly suggested that the Antillean Heptaxodontidae as usually organized may be paraphyletic, but no adequate character-based arguments have appeared that might form a strong basis for reassessment. This paper attempts to arrive at some serviceable solutions to the heptaxodontid problem by utilizing the character-rich domain of the auditory region. Thus *Amblyrhiza inundata* (St. Martin/Anguilla) and *Elasmodontomys obliquus* (Puerto Rico), the chief subjects of this contribution, have traditionally been regarded as closely related on the basis of dental features. Yet certain basicranial characters, analyzed here for the first time, reveal that *Amblyrhiza* possesses derived features of bullar development and middle-ear vascularization that are found in this specific combination only in Chinchilloidea. These features are also seen in the Mio-Pliocene Patagonian taxon *Eumegamys*, reinforcing the position that it belongs in this grouping as well. The basicranial morphology of *Elasmodontomys* is rather primitive, and where it should be placed cladistically remains indeterminate, although its likeliest position is within Octodontoidea. Although it is taken for granted that no single set of morphological features will satisfactorily capture relationships throughout a large group like Caviomorpha, the absence of basicranial characters in most morphology-based systematic discussions of these rodents is glaring. The results reported here, while suggestive in their own right, should now be tested against much larger datasets.

The amount of diversity present in the known Capromyidae-Heptaxodontidae clade...is almost as great as the diversity of all the remaining South American hystricognaths.

—C.A. Woods (1982: 390)

INTRODUCTION

This paper began as an effort to establish whether an exploration of the basicranium might help in sorting out the vexed relationships of the so-called “Antillean heptaxodontids” to other caviomorphs, living and extinct, a subject that has been of intermittent specialist interest for more than a century (see Cope, 1883; Allen, 1916; Anthony, 1916, 1918, 1920; Miller and Gidley, 1918; Kraglievich, 1926; Miller, 1930; Winge, 1941; Landry, 1957; Patterson and Wood, 1982; Woods, 1982, 1989a, 1989b, 1990; Pascual et al., 1990; Iturralde-Vinent and MacPhee, 1999; Woods et al., 2001; MacPhee and Flemming, 2003; Woods and Kilpatrick, 2005). To undertake this task required a great deal more original investigation than originally anticipated. While my objective—to “solve” the Antillean

heptaxodontid puzzle—has remained the same, and indeed makes up the core of this paper, it is hoped that the observations collected here will also be of use to workers dealing with quite different groups.

Despite pioneering morphological work on the basicranium of various relevant rodent taxa by such investigators as van der Klaauw (1931), Fields (1957), Vucetich (1975), Parent (1976, 1980, 1983), Lavocat and Parent (1985), and Bugge (1971, 1974a, 1974b, 1985), the auditory region remains a notably underutilized source of characters in systematic treatments of this group (but among recent works see Ruf et al., 2009; Pérez and Vucetich, 2011). For caviomorphs in particular, information useful for character construction and analysis is especially scanty, and truly detailed anatomical investigations exist only for taxa that have played a role in experimental studies of the auditory periphery, such as *Cavia* (e.g., Cooper and Schiller, 1975; Clements and Kelly, 1978; Begall and Burda, 2006). But even in the latter case, authors usually do not present results in a comparative framework, and, perhaps partly for that reason, they

sometimes make incorrect or dubious inductions about the homology of structures under examination. Furthermore, although some work has recently been published on basicranial fossils of extinct ctenohystericans (e.g., Bryant and McKenna, 1995; Negri and Ferigolo, 1999; Wible et al., 2005), still missing from the literature are integrated neontological investigations that might provide useful guides to morphological diversity as well as provide a basic interpretative structure. As with other mammalian groups for which these objectives have been at least partly accomplished (e.g., MacPhee, 1981; Wible, 1984, 2008; Mead and Fordyce, 2009; O'Leary, 2010), database improvement will require problem-oriented micro-anatomical and ontogenetic studies of suitable material—a long-term goal. In this contribution I lay a foundation in the form of abundantly illustrated treatments of the major basicranial attributes of selected taxa (see figs. 1–24; see also table 1), accompanied by detailed interpretation of two structures—the *tympanic fenestra* and the *posttympanic canal* (figs. 25, 26). This in turn provides a basis for extended discussions of bullar development and arterial patterning, and establishes the potential of this kind of analysis for resolving affinities (see Systematic Significance; figs. 27–29). *Amblyrhiza* and *Elasmodontomys* are the Antillean heptaxodontids best represented in museum collections, and not incidentally they are also the only ones for which basicranial fossils exist. Accordingly, they are necessarily the focal point of the descriptions and discussions presented here.

THE PROBLEM OF ANTILLEAN HEPTAXODONTIDAE

Depending on author and definition, as many as six—or as few as two—species comprise the West Indian membership of Heptaxodontidae. With one or two very dubious exceptions, all known fossils attributed to these species come from Quaternary contexts, although their history on the islands doubtless goes back much further (MacPhee, 2009). In rough order of naming and known range, currently accepted species are: *Amblyrhiza inundata* (Cope, 1868; Anguilla/

St Martin, or Anguilla¹), *Elasmodontomys obliquus* (Anthony, 1916; Puerto Rico), *Quemisia gravis* (Miller, 1929; Hispaniola), *Clidomys osborni* (Anthony, 1920; see also G. Morgan and Wilkins, 2003; Jamaica), *Xaymaca fulvopulvis* (MacPhee and Flemming, 2003; Jamaica), and, possibly, *Tainotherium valei* (Turvey et al., 2006; Puerto Rico). The first four have long been known to grossly resemble one another in exhibiting multi-lamellar or “platetooth” cheektooth organization. The affinities of the remaining two taxa, based respectively on a single, nearly edentulous jaw (MacPhee and Flemming, 2003) and a single, somewhat damaged femur not formally assigned to any family (Turvey et al., 2006), may be regarded as particularly unsettled. It is pertinent to mention that, although most platetooth taxa are founded more or less exclusively on teeth, the dentition tends to be a poor guide to higher-level relationships within Caviomorpha because of rampant convergence in dental characters (Landry, 1957: 52; see also Patterson and Wood, 1982; Woods, 1989a, 1990).

The nomina Heptaxodontinae/Heptaxodontidae have a confusing nomenclatural history. The nominotypical genus, *Heptaxodon* Anthony, 1917, is based on specimens that were shown by Stehlin and Schaub (1951), and in greater detail by Ray (1964), to be juveniles of *Elasmodontomys* Anthony, 1916. Anthony (1917: 186), who thought that in *Heptaxodon bidens* he had discovered a member of a wholly new and unusual group of caviomorphs, referred his monotypic subfamily Heptaxodontinae to Chinchillidae, together with the equally monotypic Amblyrhizinae and Elasmodontomyinae, on the ground that “[i]t is expecting too much of parallelism to so consistently develop identical tooth structure in three hystricine [i.e., hystricognath] genera.” (Even though *Heptaxodon* is now regarded as a junior synonym of *Elasmodontomys*, as Ray [1964, 1965] originally noted Heptaxodontinae remains valid as a family-group name under ICZN

¹“Anguilla” as used here refers to the subaerial landmass which would have been formed by the conjoined islands of the Anguilla Bank (Anguilla, St. Martin, St. Barts, and associated islets) during Pleistocene sealevel lowstands (McFarlane and MacPhee, 1993; McFarlane et al., 1998).

Art. 40.1 [synonymy of the type genus, validity of family-group names not affected].)

Anthony's conclusions, although very briefly stated, established the tone for much later thought on the relationships of these taxa to one another and thence to other caviomorphs (see also Anthony, 1926, 1940). When *Clidomys* and *Quemisia* were discovered in the 1920s, their general similarity to *Elasmodontomys* in dental features suggested to some authorities (e.g., Kraglievich, 1926; Landry, 1957) that they could all be accommodated in one phylogenetically and biogeographically cohesive package, together with a number of mid-Cenozoic South American taxa that also exhibited multilamellar molars and large body size. Simpson (1945) followed this line of reasoning, brigading the Antillean taxa (as Heptaxodontinae) with the mainland South American groups Potamarchinae, Eumegamyinae, and Neoepleminae, and placing the entire lot under the banner of Heptaxodontidae, superfamily Caviodea. Citing Kraglievich (1926, 1932) as authority, Simpson (1945: 212) noted that "the once very abundant, wide-spread, and varied genera here united as †Heptaxodontidae" constituted a holophyletic group, which in his concept meant that they were "related to one another and not referable, as is often done, to the Dinomyidae or other recent families." His reasoning for sharply separating heptaxodontids from dinomyids was not given, although in his classification they were placed adjacent to each other. Some later students of the group took a different stand (e.g., Fields, 1957), arguing that some of Simpson's heptaxodontids (e.g., *Tetrastylus*) could even be viewed as standing in the direct line of descent of *Dinomys*. Ray (1965) also reviewed the case for the dinomyid affinities of *Amblyrhiza* and *Elasmodontomys*.

Recent views have been more diverse, but with little character evidence in play other than that provided by the dentition, systematic assignments have remained weakly founded. Thus, Woods (1989a, 1990; see also Woods and Kilpatrick, 2005) proposed to split the Antillean taxa (his "giant hutias") into two groups, Heptaxodontinae and Clidomyinae (see also Pascual et al., 1990). His concept of Heptaxodontinae included *Quemisia*, *Elasmodontomys*, and *Amblyrhiza*, while Clidomyi-

nae was reserved for *Clidomys* alone. Earlier, Woods (1982), expanding on a view also espoused by Ray (1964, 1965), thought of possibly placing heptaxodontines and capromyids together in a separate monophyletic group, but in later papers he abandoned this conclusion and simply stated that the heptaxodontines and capromyids were very closely related, possibly sharing an unspecified common ancestor that probably lived in the West Indies in the Miocene (Woods, 1989a; Woods and Kilpatrick, 2005). Where the ancestors of that ancestor came from is unstated; in his various publications, Woods only tangentially considered Kraglievich's (1926) perceptive argument that Antillean heptaxodontids might be more closely related to certain of the large-bodied rodents of the Patagonian Neogene than to any other group. Patterson and Wood (1982) essentially threw up their hands: they were not willing to commit to any specific affiliation for Heptaxodontidae, leaving this taxon as incertae sedis as to superfamily—the only nominal family of caviomorphs that they treated in this manner.

In their classification McKenna and Bell (1997) virtually emptied Heptaxodontidae sensu Simpson and redistributed its parts among all three of the standard superfamilies. Thus, Potamarchinae and Eumegamyinae (as subfamilies within their concept of Dinomyidae) were left in Caviodea, while Neoepleminae (now as a family) was moved to Chinchilloidea. Heptaxodontidae proper was rotated into superfamily Octodontoidea (= Octodontidae, *Myocastor*, Echimyidae, and Capromyidae²) and its content reduced to *Elasmodontomys*, *Amblyrhiza*, *Clidomys*, and the poorly known Patagonian taxa *Tetrastylomys* and *Pentastylomys*. This association recalls Kraglievich's (1926, 1932) scheme in part, but seems otherwise to be their own. The inclusion of heptaxodontids within Octodontoidea echoes Landry's (1957) conclusion, later reinforced

²The family name Capromyidae is retained for the purposes of this paper, but available molecular evidence suggests that its probable fate is to be absorbed into a much-expanded Echimyidae (Woods et al., 2001; Leite and Patton, 2002; Galewski et al. 2005). The exact position of *Myocastor* within Octodontoidea is currently unclear, although on the basis of both morphological and molecular evidence it appears to be closely related to the Capromyidae/Echimyidae clade as well.

by Woods (1982), that Capromyidae—regarded as octodontoids in all recent classifications—is the sister group of heptaxodontids. More recently, Negri and Ferigolo (1999) have relimited Neopiblemidae to include *Neopiblema*, *Phoberomys* (a eumegamyrine according to McKenna and Bell [1997]), and *Eusigmomys* (a potamarchine according to McKenna and Bell [1997]). Classificatory shufflings of this magnitude may well be warranted, but they also indicate that consensus on the phylogenetic placement of these rodents has not been reached.

MATERIALS AND METHODS

COMPARATIVE SET

The comparative set (appendix 1) assembled for this study includes representatives of all currently recognized ctenohystrican families having extant representation (i.e., Ctenodactylidae + all families traditionally placed in Hystricognathi; see Huchon and Douzery, 2001; Huchon et al., 2007; Churakov et al., 2010). Although the concept that Caviomorpha is strictly monophyletic has been challenged from time to time, at present the possibility of paraphyly seems remote and I do not deal with it further here (Nedbal et al., 1994; Huchon et al., 2007; Carleton and Musser, 2005; but see Jenkins et al., 2005; Coster et al., 2010).

As already illustrated, there is a continuing flux in ctenohystrican systematics regarding sister-group relationships, organization of superfamilies, and the positioning of a number of fossil taxa, and doubtless this grouping will undergo further internal changes with the application of new data sources and new methodologies. However, to ease the need to use a plethora of possibly evanescent names, the supergeneric entities presented in this paper generally follow the most recent version of the classification of Ctenohystrica as provided by the Paleontology Database (currently housed at <http://museum03.museumwww.naturkundemuseum-berlin.de/cgi-bin/bridge.pl>), with modifications where noted. For simplicity I maintain the conventional division of extant caviomorphs into the four superfamilies Erethizontoidea, Caviioidea, Chinchilloidea, and Octodontoidea.

The hystricognaths of Eurasia and Africa present a more complex picture; at present I follow the convention of simply grouping Bathyergidae, Thyronomyidae, Hystrichidae, Petromuridae, and Diatomyidae under the banner of Phiomorpha. Ctenodactylidae is traditionally left outside this scheme, as here, within its own superfamily.

The total number of specimens per taxon examined (see appendix 1) is necessarily small because whenever possible I selected “no data” skeletons and skulls with broken basicranial regions for study and dissection. Notes on the dissection of the infratemporal fossa and sidewall of the auditory region of *Dinomys branickii* AMNHM 201638 are presented separately (see Original Observations).

With respect to the basicrania of fossil dinomyids and other extinct chinchilloids, which are of special interest here, published observations of any sort are rare and do not shed much light on the interpretation of the specific structures of interest here. For example, in regard to the feature here named the tympanic fenestra, Fields (1957: 282) notes for the La Venta taxa *Olenopsis* and *Scleromys* only that the “accessory rounded ventral opening [is] present as in *Dinomys*.” Negri and Ferigolo (1999: fig. 14) mention the presence of another feature, an apparent posttympanic foramen, on an excellent skull of *Neopiblema ambrosettianus*, but they allude to it as a supernumary “forame parum dos ramos do nervo facial (VII)?”—an occurrence otherwise unknown in rodents. Vucetich (1975), who described middle ear features of the related genus *Perimys incavatus*, noted the presence of the tympanic fenestra as well as some other systematically pertinent basicranial features. The partial skeleton of Late Miocene *Phoberomys pattersoni*, a truly giant megafaunal taxon recently analyzed by Horovitz et al. (2006; see also Sánchez-Villagra et al., 2003), includes cranial material. However, the basicranium is not in a condition in which it can be profitably studied (M. Sánchez-Villagra, personal commun.). The related, and even larger, species *Josephoartigasia monesi* (Rinderknecht and Blanco, 2008) is represented by a skull, but no description of the auditory region has yet been published. Fortunately, during the course of this study an opportunity arose to

TABLE 1
Abbreviations

INSTITUTIONAL AND OTHER	
AAHS	Anguilla Archaeological and Historical Society
AMNHM	American Museum of Natural History, Department of Mammalogy
AMNHVP	American Museum of Natural History, Department of Vertebrate Paleontology
ICZN	International code of Zoological Nomenclature, 4th ed.
MLP	Museo de La Plata, Departamento Científico de Paleontología de Vertebrados
USNMM	United States National Museum of Natural History, Division of Mammals
ANATOMICAL	
alisph can	alisphenoid canal
ant crus	anterior crus (of ectotympanic)
ant lat pr	anterolateral process
ant med pr	anteromedial process
aper can tens tym m	aperture of canal for tensor tympani muscle
aper tub can	aperture of tubal canal
aud bulla	auditory bulla
aud tub	auditory tube
bcap fen	basicapsular fenestra
BOCC	basioccipital
bocc-bsph syn	basioccipital-basisphenoid synchondrosis
br	broken
can auric ram vag n	canal for auricular ramus of vagus nerve
can chor tym	canaliculus for chorda tympani
caud dig m	caudal head of digastric muscle
can tym n	canaliulus for tympanic nerve
caud tym pr petr	caudal tympanic process of petrosal
coch can	cochlear canaliculus
dist expan	distal expansion (of tympanic fenestra)
ECT	ectotympanic
ecto/ecto sut	ectotympano-ectotympanic suture
ecto/petr sut	ectotympano-petrosal suture
endocran surf	endocranial surface
endolym duct	endolymphatic duct
EOC	exoccipital
epitym rec	epitympanic recess
ext car a	external carotid artery
fac n	facial nerve
fac can	facial canal
for chorda tym	foramen for chorda tympani
for lacer	foramen lacerum (= or incl. piriform fenestra)
for oval	foramen ovale
for rot	foramen rotundum
fos fen coch	fossula fenestrae cochleae
glas for	glaserian foramen
gr aud tube	groove for auditory tube
gr hyoid	groove for hyoid apparatus (tympanohyal/stylohyal)

TABLE 1
(Continued)

gr inf petr sin	groove for inferior petrosal sinus
gr mand n	groove for mandibular nerve
gr post auric a	groove for posterior auricular artery
gr tens tym m	groove for tensor tympani muscle
gr tym n	groove for tympanic nerve
hypogl for	hypoglossal foramen
INC	incus
inf petr sin	inferior petrosal sinus
int acous meat	internal acoustic meatus (or canal)
int jug v	internal jugular vein
JU	jugal
jug for	jugular foramen
MALL	malleus
MAND	mandible
mass m	masseter muscle
mast	mastoid
mast for	mastoid (venous) foramen
mast pr	mastoid process
maxill a	maxillary artery
meat innom for	meatal innominate foramen (-ina)
meat innom v	meatal innominate vessel(s)
OCC	occipital
occ cond	occipital condyle
PAR	parietal
parocc pr	paroccipital process
perilym duct	perilymphatic duct
petr sqam sin	petrosquamous sinus
post auric a	posterior auricular artery
post crus	posterior crus (of ectotympanic)
posttym can	posttympanic canal
posttym for	posttympanic foramen
(prim) ext acous meat	(primitive external acoustic meatus or canal)
prom	promontorium
PTE	pterygoid
retroart for	retroarticular [= postglenoid] foramen
rev	reversed
sec	secondary
SOC	supraoccipital
sphenorb for	sphenorbital foramen
SQU	squamosal
stap fos	stapedial fossa
stylohy m	stylohyal muscle
stylomast for	stylomastoid foramen
sulc tym n	sulcus for tympanic nerve
tens tym m	tensor tympani muscle
tub can	tubal canal
tym cav	tympanic cavity
tym col	tympanic collar
tym fen	tympanic fenestra
tymhy	tympanohyal (noted when prominent)
ventr cl	ventral cleft
ven for	venous foramen
X n	vagus nerve
XI n	(spinal) accessory nerve

study the basicranium of MLP 41-XII-13-237 (figs. 9–11), a well-preserved partial skull of the Pliocene dinomyid *Eumegamys* (= *Eumegamysops*; Alvarez, 1947; Fields, 1957). While not a substitute for the much larger study required of Neogene chinchilloids in general, it is hoped that the evaluations presented here will lay a proper basis for further work and give some indication of what may be accomplished with appropriate material.

Most anatomical structures and ontogenetic terms mentioned in the text are defined in MacPhee (1981), which should be consulted for details not covered here. For accessing general mammalian cranial morphology or finding answers to specific queries, also helpful are databases and published papers viewable on the Morphobank site (www.morphobank.org). MacClade 4 (Maddison and Maddison, 2003) was utilized for the character optimizations presented in figures 27–29.

HYPODIGM OF *AMBLYRHIZA INUNDATA*

AMNHVP and AAHS hold almost all of the available material of this species, whose distribution was limited to the major islands of the Anguilla Bank (Anguilla and St. Martin). Naturalis (National Natural History Museum, Leiden) also possesses a small number of *Amblyrhiza* fossils, as detailed by Schreuder (1933; see also van der Geer et al., 2010). AMNHVP specimens largely derive from Edward Drinker Cope's personal paleontological collection, which was purchased by the AMNH in the 1890s. Cope's *Amblyrhiza* specimens were, in turn, originally collected for him by H. van Rigersma, a Dutch colonial physician who for many years provided interested scholars in the United States and Europe with natural history specimens from several of the northern Lesser Antilles (Cope, 1883; McFarlane and MacPhee, 1989). The AMNH mammalogist Harold E. Anthony, who visited St. Martin and Anguilla in 1926 for the express purpose of collecting additional remains of *Amblyrhiza*, recovered a number of specimens for this museum in cave localities on both islands. Although he never published on these fossils, his fieldnotes (Anthony, MS.) are available in the Mammalogy archives.

The AAHS collection was amassed between 1988 and 1995 in cooperation with Donald McFarlane (Claremont McKenna College) and various AAHS members (for locality and other information, see McFarlane and MacPhee, 1989; Biknevicius et al., 1993).

Although reasonably good specimens of the jaw, rostrum, palate, auditory region, and many isolated teeth are available for study, there are no intact skulls. Much the same applies to the postcranium: although proximal and distal ends of most long bones exist, there are no complete specimens. Some of the long bones in Cope's original collection are broken in a way that suggests that they may have been intact when recovered during phosphate mining operations, but were poorly handled thereafter.

HYPODIGM OF *ELASMODONTOMYS OBLIQUUS*

Most of the known specimens of this species are housed in the AMNHVP, with smaller collections in the Florida Museum of Natural History, Museum of Comparative Zoology at Harvard, and elsewhere. Remains of this rodent were first encountered in 1915, during the course of the New York Academy of Sciences' wide-ranging scientific survey of Puerto Rico and the Virgin Islands (Woods, 1996). During the following year, H.E. Anthony made prodigious collections in caves in the western and central parts of the island; virtually all of the AMNHVP specimens of *Elasmodontomys* derive from his fieldwork (Anthony, 1918; Woods, 1996). Since then few additional specimens have come to light, although with renewed interest in active collecting of extinct West Indian mammals (e.g., Turvey et al., 2006, 2007), major new discoveries of material will doubtless occur. The hypodigm for this species is extensive and, unlike that for *Amblyrhiza*, contains large numbers of complete specimens, including postcranials and skulls.

CHARACTER ANALYSIS

Table 2 provides a list of characters and recognition criteria for discriminating among the character states of interest here. Character states have been formulated on the basis of the morphological observations provided

TABLE 2
List of Basicranial Characters and States

Character 1: Absence/presence of tympanic fenestra	
0, absent or aperture restricted to foramen/foramina for meatal innominate vessels.	Ventral margin of meatus is complete, no ectotympano-ectotympanic suture; one or more small, rounded apertures for meatal innominate vessels normally present.
1, tympanic fenestra present as notch (bridged or unbridged).	Ventral margin of meatus clefted, in form of a short, narrow gap with ragged margins and little or no distal expansion. In definitive condition cleft may be partly covered by short outgrowths of bone, but lengthy suture not present.
2, tympanic fenestra present as large dehiscence, isolated from meatus by suture-delimited area.	Ventral margin of meatus in young stages interrupted by ventral cleft, characteristically long and ending in large distal expansion. In ontogenetically definitive condition, margins of cleft approximate to form an ectotympano-ectotympanic suture, thus osteologically separating fenestra from meatus.
Character 2: Absence/presence of posttympanic foramen	
0, absent.	No significant vascular apertures on posterior bullar wall (apart from meatal innominate foramina).
1, present, positioned on external bullar wall.	Foramen is fully exposed; may lie in close relation to tympanohyal or stylomastoid foramen but not within latter.
2, present, positioned in or connects with stylomastoid foramen.	Foramen situated on lip of (or within) stylomastoid foramen, or opens into latter (provisional identification).
Character 3: Absence/presence of posttympanic canal	
0, absent.	No canal or septum as described below.
1, present.	Discrete bony canal or grooved septum running intratympanically, in close relation to crista tympanica, from posttympanic foramen to area of cochlear window, where it terminates or can no longer be followed.
Character 4: Absence/presence of pessulus traversing stapedia obturator foramen	
0, absent.	
1, present.	

under Original Observations (see below), and are referenced in the text by a consistent convention. “C1:2”, for example, refers to “Character 1: Absence/presence of tympanic fenestra,” with character state 2, “tympanic fenestra present as large dehiscence, isolated from meatus by suture-delimited area” determined on the basis of associated recognition criteria. Consult figures 27–29 to see how character distributions map onto a predetermined scaffold tree. Although I have framed the interpretation of character states in a developmental framework where feasible, I emphasize that all character states should be understood to refer to adult or definitive conditions.

TYMPANIC FENESTRA AND POST-TYMPANIC VASCULAR FEATURES

INCIDENCE AND ONTOGENY OF THE TYMPANIC FENESTRA

Although the structure identified here as the tympanic fenestra is described under a variety of names in the mammalian morphological literature, its anatomy and development have

been traced in detail only in *Homo sapiens* (most frequently under the names *foramen tympanicum* or *foramen of Huschke*; e.g., Wang et al., 1991; Lacout et al., 2005). Gacek (1975: 363), who gave a brief description of this feature in adult *Cavia*, describes it as the “ventral tympanic canal” (cf. “ventral accessory opening” of Fields [1957]; “segundo meato alargado” of Vucetich [1975]). However, I prefer *tympanic fenestra* because this dehiscence rarely resembles a typically rounded foramen or canal. Although it is unknown whether the persistent tympanic fenestra affects audition in any taxon that exhibits it, it is noteworthy that this feature is typically situated directly across from the umbo, site of the tympanic membrane’s maximum amplitude.

Viewed over the timescale of ontogeny, the part of the fetal mammalian ectotympanic that bears the tympanic membrane (crista tympani) stops growing relatively early, but in most mammals the inner and outer margins of the original crura continue to expand radially along the fibrous membrane, albeit to varying degrees in different clades (MacPhee, 1981; MacPhee and Cartmill,

1986). In all mammals, lateral growth frames the bony external acoustic meatus more or less completely; in rodents and many other groups, growth along the ectotympanic's medial aspect also produces most or all of the auditory bulla. The ectotympanic always ossifies as a membrane bone in mammals and never exhibits primary or secondary cartilage (MacPhee, 1981). Ossification defects like the tympanic fenestra therefore cannot be ascribed to imperfect replacement of a cartilaginous preformation.

The conventional description of fenestral formation in the human specifies that, during the first year of life, the rostral and caudal crura of the U-shaped ectotympanic send out platelike expansions that meet centrally to form the floor of the developing external acoustic meatus and tympanic cavity (Anson et al., 1955). Typically, a small, unossified zone remains for a time between these expansions. The gap usually disappears by the age of five, but a persisting dehiscence is not uncommon. Lacout et al. (2005) found a patent hole in 4.5% of their sample of 103 temporal bone examinations.

Lacout et al. (2005) also state that the fenestra of *Homo* does not transmit anything at any stage of development. With regard to large neurovascular structures, this also appears to be the case in ctenohystriacans. However, in a number of taxa in this group, fine vascular perforations occur within the same circumscribed region on the lateral bullar wall as the patent tympanic fenestra found in other members of this clade. This suggests that the vessels in question are probably a reasonably constant feature of lateral wall development. Whether or not they are eventually entrapped in bone depends on the nature of final ectotympanic development in this region. On incompletely cleaned skulls, dried vasculature may often be found in the immediate vicinity of the meatus and outer rim of the tympanic membrane. In *Homo*, these areas are fed by branches from the posterior auricular, superficial temporal, and maxillary arteries; as it is not evident which of these major trunks send emissaries to the lateral bullar wall in ctenohystriacans, here they will simply be designated as meatal innominate vessels. They are not homologous with the ramus

posttympanicus (see below), which, when definitely present, appears to supply a different area, one situated well within the middle ear cavity.

I emphasize that, although it is often continuous with the porus meatus, the fenestra is not an empty gap. In life it always seems to be occluded or walled off by a plug of meatal soft tissues ultimately derived from the fibrous membrane of the tympanic cavity (or the membranous meatus, with which the fibrous membrane is continuous). In several incompletely cleaned osteological specimens utilized for this study, the plug displays—unsurprisingly, given its continuity with the meatal lining—structures suggestive of glandular tissue (Gacek, 1975; cf. fig. 25, *Dasyprocta punctata* AMNHM 41394).

If every occurrence of an aperture in the lateral bullar wall were counted as a tympanic fenestra, character discrimination would be pointless. Accordingly, cases in which the tympanic fenestra is reduced to a single, rounded vascular foramen for innominate vessels (e.g., *Myocastor coypus* AMNHM 80097; fig. 22A) are scored the same as complete absence (C1:0). (Although the point is of no direct pertinence here, in this scheme *Homo* would also be scored as C1:0.)

Although obliteration of the tympanic fenestra is a normal aspect of temporal bone ontogeny in *Homo*, its incidence in the ontogeny of most other mammals is simply unknown. Part of the reason for this is that previous investigators have noted the presence of a fenestra only in instances in which it was comparatively large. Van der Klaauw (1931), for example, described finding it as an opening or ventral cleft in the meatal margin only in certain members of extant Herpestinae, Canidae, and Caviomorpha. Reports of this aperture in fossil mammals are even rarer; in one of the few instances on record, Simpson (1967: 222) described what appears to be a patent fenestra (as a “deep narrow notch”) in the meatal floor of the trigonostyloid astrapothere *Trigonostylops wortmani*.

In the specific case of caviomorphs, van der Klaauw (1931) documented a certain amount of variation in fenestral shape. The fenestra often has the form of an irregular gap (distal expansion of this paper) at the end of a narrow slit (ventral cleft of this paper) in

the lateral bullar wall, but the expression of these features varies. Thus, van der Klaauw (1931) noted that *Hydrochoerus*, *Dasyprocta*, and *Dinomys* display a prominent ventral cleft that extends through the meatal lip, while in *Cavia*, *Lagostomus*, *Chinchilla*, and *Lagidium* “both margins of the incision are connected distally, thus forming an aperture” (van der Klaauw, 1931: 161) or an external acoustic meatus “doble con los orificios separados” (Vucetich, 1975: 488). In *Myocastor*, “only a notch (*Einschnitt*) in the border of the meatus is found, which by further growth is closed by the union of the margins [of the ectotympanic]. The development is much the same in man.” Although his wording is not explicit, van der Klaauw appears to have concluded that ectotympanic development was actually rather similar in all of these cases, the only differences being in the details. In one sense this is correct, but, as we shall see, variation is complex enough to warrant the discrimination of at least three character states (table 2). In evaluating these states, a certain amount of emphasis is placed on how the margins of the dehiscence mature. The definitive condition of the meatal area is, of course, achieved just as it is elsewhere on the bulla, i.e., by the deposition of bone matrix along existing bone margins on the scaffolding provided by the fibrous membrane. This is fully analogous to the closure of cranial fontanelles by mineralization along the primitive ectomeninx (MacPhee, 1981). Typically, however, approaching bone territories on the cranial vault eventually meet and form sutural tissues; in the case of the closure of the tympanic fenestra, sutural formation is seen much more rarely, probably because the single element involved (the ectotympanic) forms an internal suture only under special conditions. Unfortunately, very young specimens with largely unossified skulls are rarely found in traditional osteological collections, and thus the earliest phases of ectotympanic development in the taxa described here remain partly conjectural.

POSTTYMPANIC FORAMEN, POSTTYMPANIC CANAL, AND RAMUS POSTTYMPANICUS

The posttympanic foramen and canal (C2, C3) are recognized as anatomical entities for

the first time in this paper. Only four taxa—*Amblyrhiza inundata* (figs. 1, 4), *Dinomys branickii* (figs. 12–14), and the extant erethizontids *Coendu mexicanus* and *Erethizon dorsatum* (fig. 19)—in the comparative set were found to exhibit both the external aperture (posttympanic foramen, C2:1) and the intratympanic conduit related to it (posttympanic canal or septum, C3:1). (The foramen is present in *Eumegamys paranensis*, but the canal could not be identified with certainty.) The posttympanic foramen is situated on the external bullar wall, slightly posteroventral to the stylomastoid foramen in *Dinomys*. The posttympanic canal is a large, discrete tube or, sometimes, a grooved intratympanic septum that runs in close relation to the bony frame encompassing the tympanic membrane, to terminate in the vicinity of the stapedius fossa or cochlear windows. That these structures transmit an artery (here named the *ramus posttympanicus*) is conclusive for extant *Dinomys* (see Original Observations) but inferential for extinct taxa such as *Amblyrhiza* and *Eumegamys*. The posttympanic canal should not be confused with the canaliculus chordae tympani (MacPhee, 1981); the latter nerve also passes freely into the rear part of the tympanic cavity, but then wends its way through the ossicular chain, unlike the posttympanic canal. Consideration of the possible homologies of the *ramus posttympanicus* is left for the last part of this paper.

Some extant members of Chinchillidae were also found to exhibit a probable posttympanic foramen, in or near the stylomastoid foramen (C2:2), but because they lacked an identifiable posttympanic canal within the middle ear, the presence and destination of the vessel transiting the foramen must remain somewhat uncertain until dissection evidence is available. The true stylomastoid artery may be implicated here instead.

The posttympanic canal is clearly vascular and therefore not the homolog of the meato-cochlear bridge formed by tympanohyal-mastoid fusion, as described by Meng (1990) for the Eocene North American protrogomorph *Reithroparamys*. However, because the true posttympanic foramen is normally situated close to the base of the tympanohyal, it could easily be (and perhaps

has been) misinterpreted as a sheath for that structure.

Notice is also made of the occurrence of pessuli (C4),³ or small struts of bone within the obturator foramen of the stapes that are interpreted by some authors (e.g., Guthrie, 1963) as homologous with the bony stapedial canal seen in some primates and a variety of other, mostly small, mammals. Pessuli are thus relevant to the question whether parts of the primitive stapedial system persist in hystricognaths (see appendix 2).

ORIGINAL OBSERVATIONS

BASICRANIAL MORPHOLOGY OF *AMBLYRHIZA INUNDATA*

Two specimens of this species preserve the auditory region in substantially complete form. The first, AAHS 95044, is an isolated left tympanopetrosal from Tanglewood Cave, Anguilla, collected by Don McFarlane and the author (see McFarlane and MacPhee, 1989). The specimen includes the floor of the ectotympanic bulla but lacks the lateral parts of the external acoustic canal and related structures. The tympanic floor was intact at the time of discovery, but it has since been dissected (by carving a "window" into it) to facilitate the present investigation (figs. 1–3). The other specimen, AMNHVP 11842, is a basicranial fragment consisting of the left petrosal, exoccipital, and a portion of the ectotympanic bulla with the meatal region preserved (figs. 4, 5). This fossil, part of the AMNHVP Cope collection, lacks a stated provenance but was presumably collected by van Rigersma on either St. Martin or Anguilla. It is significantly larger than AAHS 95044 and somewhat differently proportioned, suggesting that the former specimen may have belonged to a juvenile animal. Or the difference may be a consequence of significant variability in body size in this species, evidence for which is discussed in detail by Biknevicius et al. (1993). Although for the purposes of this paper the two

specimens were photographed in broadly similar aspects, slightly different viewing angles were chosen so that complex features could be seen in at least one ear region.

In ventral aspect the banana-shaped bulla of *Amblyrhiza* presents three projections. The most prominent is the external acoustic canal, which in AMNHVP 11842 is drawn out into a long tube that (when intact) would have projected upward and slightly backward (fig. 4). The other two projections (anteromedial and anterolateral processes) are simple pneumatic evaginations of the rostral end of the bulla. The more medial of the two may have articulated with the pterygoid or possibly served as an attachment point for palatal musculature (tensor veli palatini muscle). There is no indication that the lateral margin of the porus meatus supported accessory bones of the sort found in *Cavia* (van der Klaauw, 1931; Gacek, 1975), although the available material is not well enough preserved to decide this point. In the more complete specimen, AMNHVP 11842, both the mastoid and occipital are damaged, but judging from remaining surfaces both participated in what must have been a markedly robust paroccipital process (fig. 4).

Four prominent apertures or channels for vasculature and nerves can be identified in their expected positions in AMNHVP 11842 (figs. 1, 4)—the inferior petrosal sinus and the stylomastoid, hypoglossal, and jugular foramina. The stylomastoid foramen is situated in an elongated groove, relatively high on the sidewall of the cranium and immediately posterior to the posterior crus of the ectotympanic (or bone derived therefrom). AAHS 95044 (fig. 1), photographed from a more medial angle and without obscuring occipital material, displays several other small apertures, including the cochlear canaliculus for the perilymphatic duct and the canal for the tympanic nerve. Posteriorly, the line of petromastoid-exoccipital contact leaves space for venous drainage of the petromastoid, as in extant caviomorphs (e.g., *Myocastor coypus*, fig. 22B). Nearby there is a tiny channel (?mastoid canaliculus for the auricular ramus of the vagus nerve), passing obliquely through bullar material. (No exit foramen was identifiable on the bullar wall, but equally there is no indication that the

³"The stapes in [*Cavia*] is formed with slender crura, constituting a rounded arch, through which an osseous bolt passes, so as to rivet it to its situation. This bolt I have named pessulus" (Carlisle, 1805: 204). The notion that the pessulus prevents the stapes from falling into the vestibule is obviously fanciful, but the name has stuck.

channel actually perforated the tympanic cavity.)

The posttympanic foramen is situated low on the lateral aspect of the bulla, a short distance from the stylomastoid foramen and near a shallow dimple that may have lodged the tympanohyal-stylohyal articulation. This foramen opens directly into the posttympanic canal, discussed in detail below.

Of particular interest is the fact that both specimens display a teardrop-shaped tympanic fenestra, resembling that of certain extant chinchillids and dinomyids and positioned at the bottom of a deep fossa (figs. 2, 4). In AAHS 95044 the fenestra narrows into an ectotympano-ectotympanic suture, still partly open at the site of the original ventral cleft. In AMNHVP 11842 a more advanced stage of closure is seen, with the cleft completely closed. The suture line can still be identified, externally as well as internally, by a raised seam on the meatal floor (fig. 5).

Since the bullar floor was already broken in AMNHVP 11842, allowing inspection of most of the middle ear cavity, an equivalent area was removed from the floor of AAHS 95044 to permit comparison (see figs. 1, 4). In both specimens the tympanic cavity proper is undivided, although several low septa are present. Thus, the deep trough and low partial septum in the anteromedial quadrant of the tympanic roof (fig. 4) marks the passageways for the auditory tube and the belly and tendon of tensor tympani muscle. The cochlear promontorium is relatively low (i.e., not towered, as in *Cavia*, *Dasyprocta*, and some other cavioids) and unmarked by large sulci or cristae. No aperture for the tympanic nerve can be detected in either specimen, although it probably entered the tympanic cavity near the posterior pole of the promontory, as is typical of placentals (MacPhee, 1981). Epitympanic pneumatization of the dorsal part of the auditory capsule is exceptionally extensive in *Amblyrhiza*. Although no intact skulls of this taxon are known, inspection of isolated cranial fragments indicate that much of it was massively pneumatized, perhaps in much the same manner as the skull of *Eumegamys* (see below).

The incus-malleus of AAHS 95044 (not illustrated), a fused structure in many but not

all adult ctenohystriacans (Patterson and Wood, 1982), was retrieved when the bullar floor was opened. The stapes was not in evidence; it may have fallen out earlier through the damaged epitympanic recess. There is no indication that *Amblyrhiza* possessed a pessulus.

In AAHS 95044 the crista tympani is carried on a lengthy cylinder of bone that projects deeply into the tympanic cavity (fig. 1). Presumably, as the bulla inflated the segment of the ectotympanic supporting the tympanic membrane maintained both its proportions and its ontogenetically primitive position near the cochlea. In van der Klaauw's (1931: 201) terminology the cylinder would be an *eminencia cristae tympanicae*, but I propose the simpler and more descriptive phrase *tympanic collar* (diameter, 7.5 mm in AMNHVP 11842) to refer to the expanded, intratympanic portion of the ectotympanic. (This structure in caviomorphs is also morphologically equivalent to the spurious *ossified anulus membrane* of lemurs, as MacPhee and Cartmill [1986] originally established.) Also worth noting is the large number of small, apparently imperforate septa adorning the collar's periphery. Their function is obscure, although some may have conducted blood vessels (?meatal innominate vasculature).

The degree of obliteration of the intratympanic ectotympano-petrosal suture is widely variable among hystricognaths. In the available specimens of *Amblyrhiza*, fusion is extensive: the medial bullar wall is seamlessly continuous with the promontorium in ventral aspect. Externally, the only indication of the original site of ectotympano-petrosal contact is a narrow crevice defining the border of the anteromedial part of the tympanic roof (which must therefore in part be derived ontogenetically from ectotympanic material; fig. 3).

Three bony tubes pass through or along the tympanic roof. In homological terms the least problematic to identify is the broad prominence of the facial canal, which travels through the rear part of the cavity (fig. 1). The second canal lies anterolaterally, and can be traced from the anterior margin of the epitympanic recess to the lateral aspect of the tympanic roof. The canal passes through the

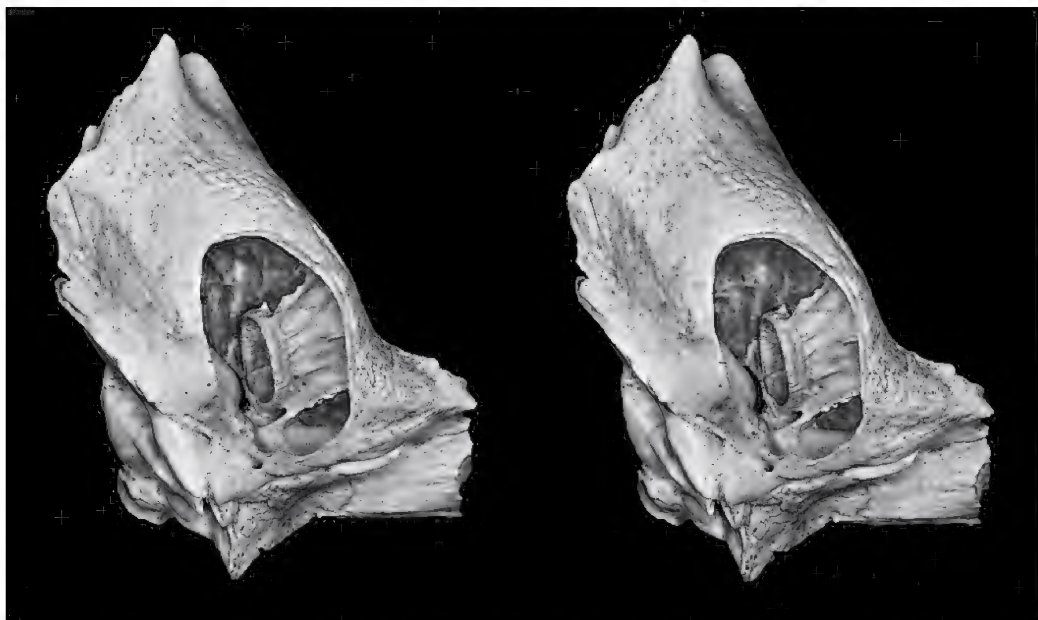


Fig. 1. *Amblyrhiza inundata* AAHS 95044, left auditory region after removal of tympanic floor; stereopair view (with key, opposite page) in ventromedial aspect, showing tympanic collar and posttympanic canal.

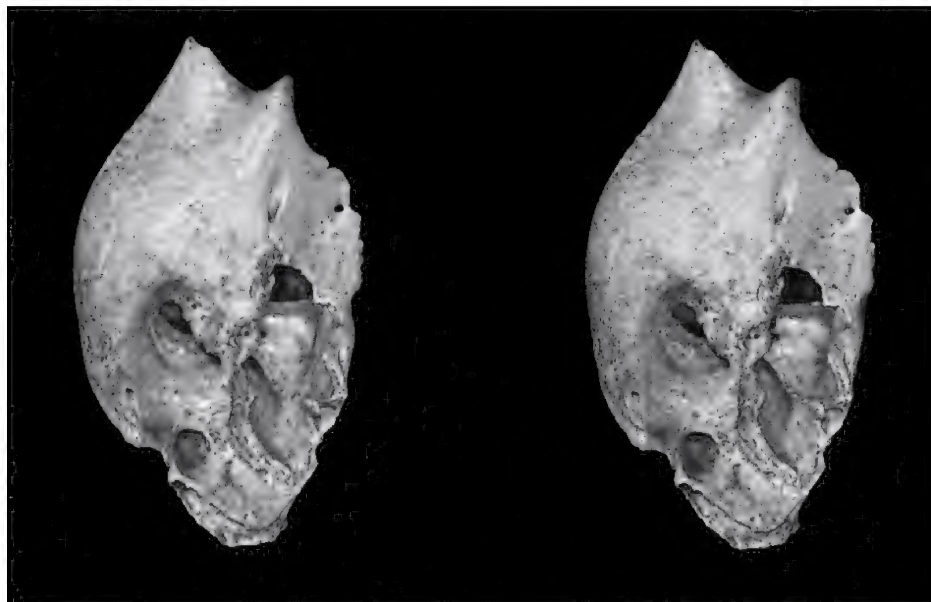


Fig. 2. *Amblyrhiza inundata* AAHS 95044, left auditory region before removal of tympanic floor; stereopair view (with key, opposite page) in lateral aspect. Hatchure, broken wall of external acoustic meatus; asterisk, dorsal rim of external acoustic canal.

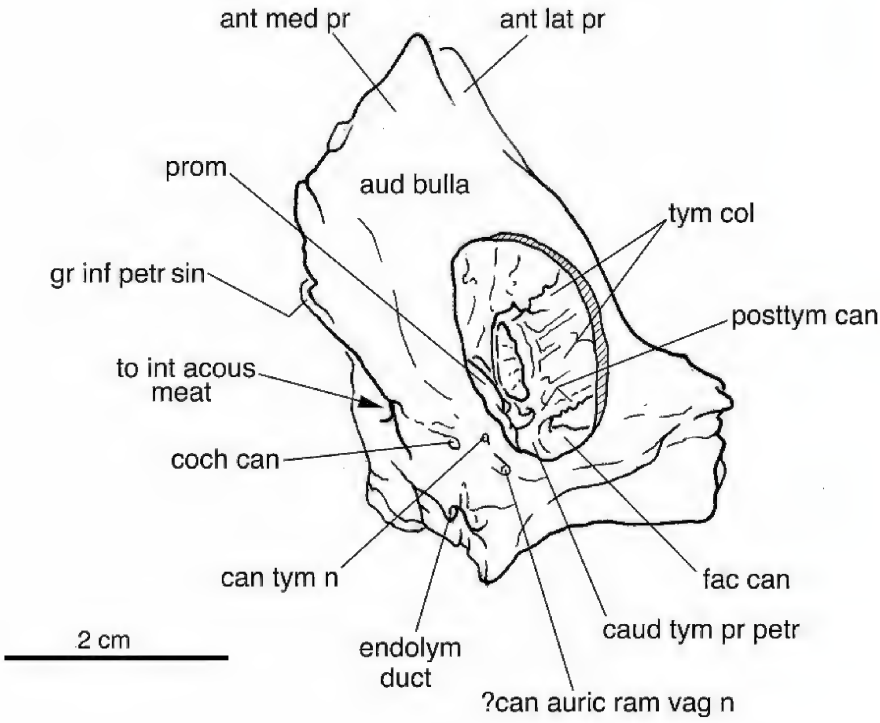


Fig. 1. Continued.

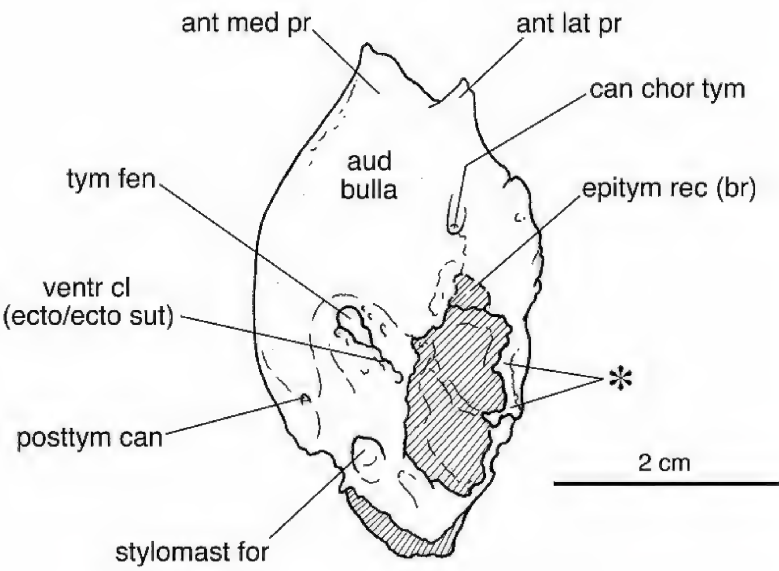


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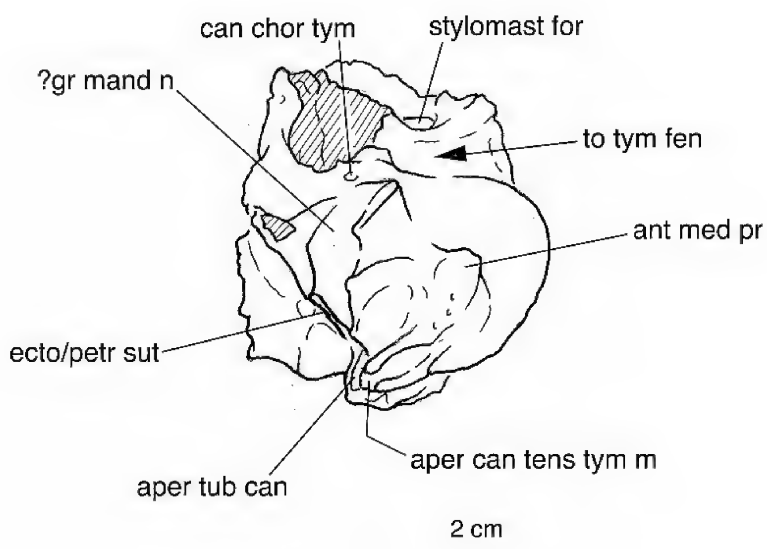
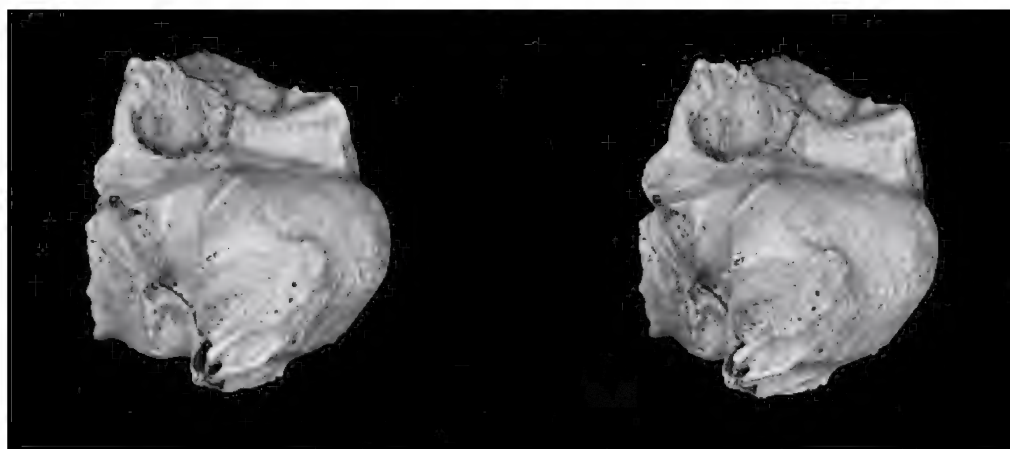


Fig. 3. *Amblyrhiza inundata* AAHS 95044, left auditory region before removal of tympanic floor; stereopair view with key, in rostral aspect. Hatchure, broken wall of external acoustic meatus. Arrow, position of tympanic fenestra (out of view).

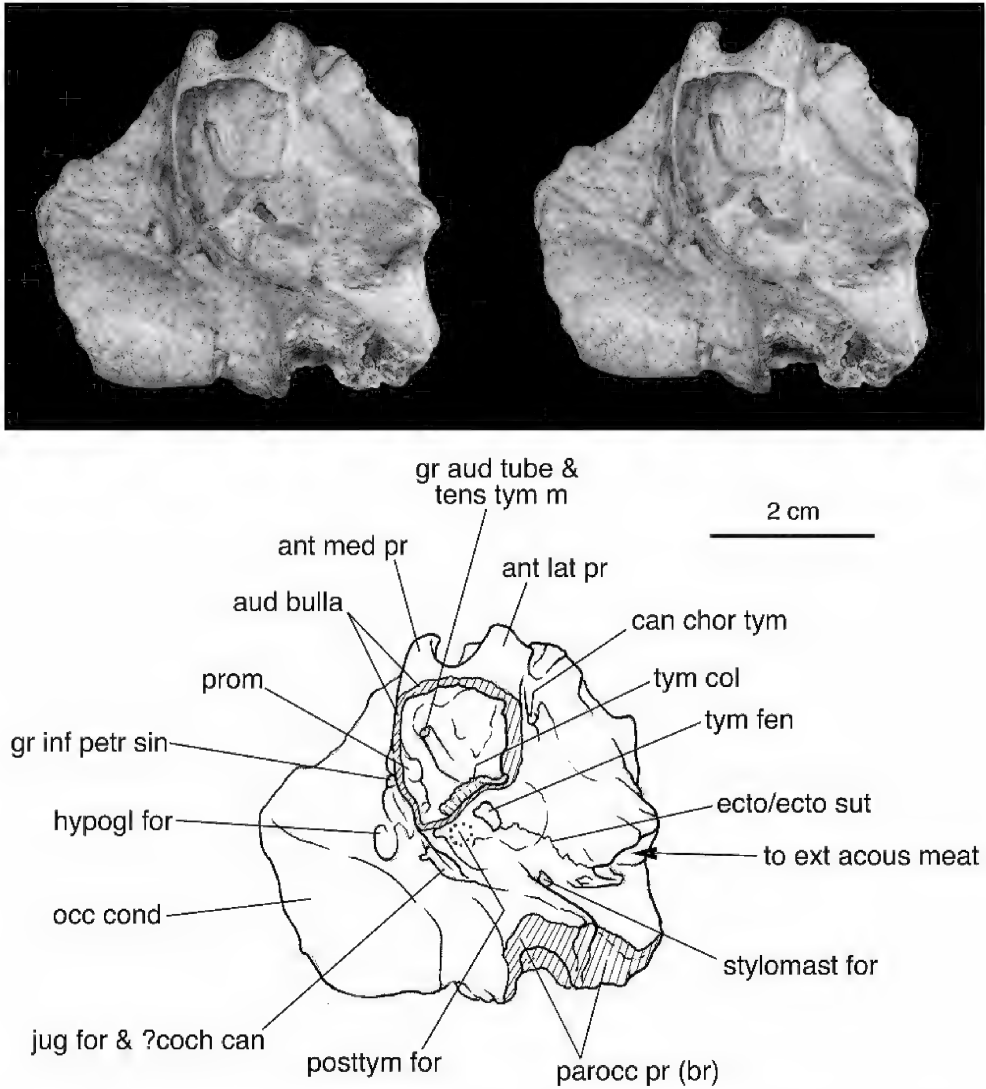


Fig. 4. *Amblyrhiza inundata* AMNHVP 11842, left auditory region; stereopair view (with key) in oblique ventral aspect. The condition of the specimen did not permit thorough cleaning of the tympanic cavity. Cochlear canaliculus for the perilymphatic duct could not be identified with certainty. In this orientation the posttympanic foramen is mostly hidden; the leader points to its general location (circle of dots in key diagram).

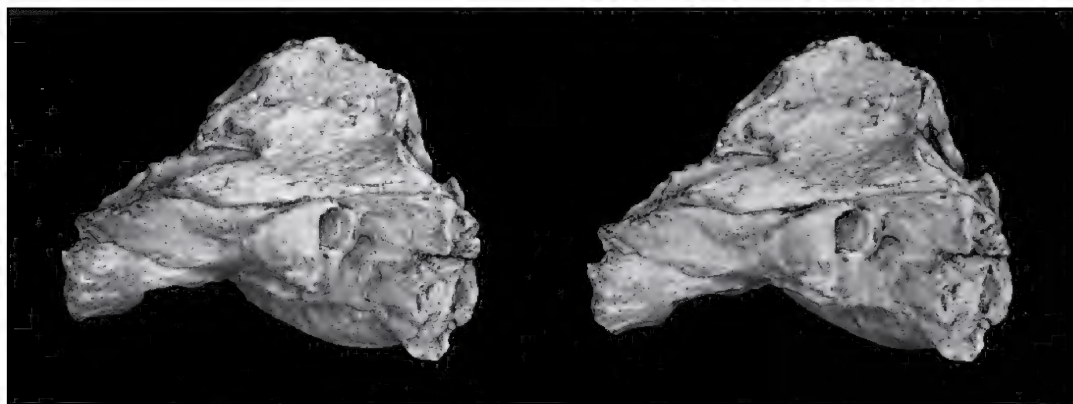


Fig. 5. *Amblyrhiza inundata* AMNHVP 11842, left auditory region; stereopair view (with key, opposite page) in oblique lateral aspect. Asterisk, raised seam of ectotympano-ectotympanic suture continued onto floor of external acoustic meatus. Position of the posttympanic foramen is hidden by the projecting external acoustic canal. Paroccipital process is heavily pneumatized, in contrast to conditions in *Eumegamys* (see text).

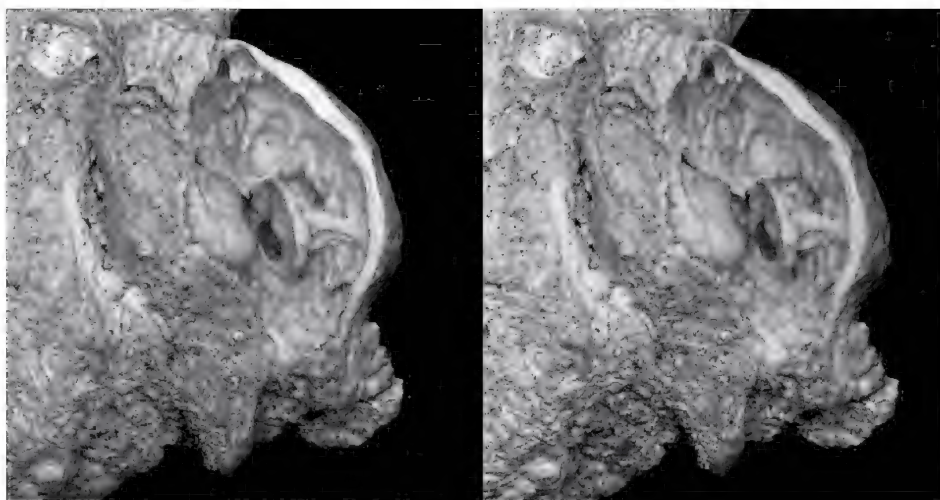


Fig. 6. *Elasmodontomys obliquus* AMNHVP 14171 (holotype), left auditory region; stereopair view (with key, opposite page) in ventral aspect. Although this specimen is poorly preserved, it is possible to identify ectotympano-petrosal contact on the medial aspect of the promontorium (asterisk). The heavily-sculpted bullar wall is exceptionally thick, as in some octodontoids (e.g., *Geocapromys*, fig. 21). There is no indication of a posttympanic canal like that of *Amblyrhiza* (fig. 1).

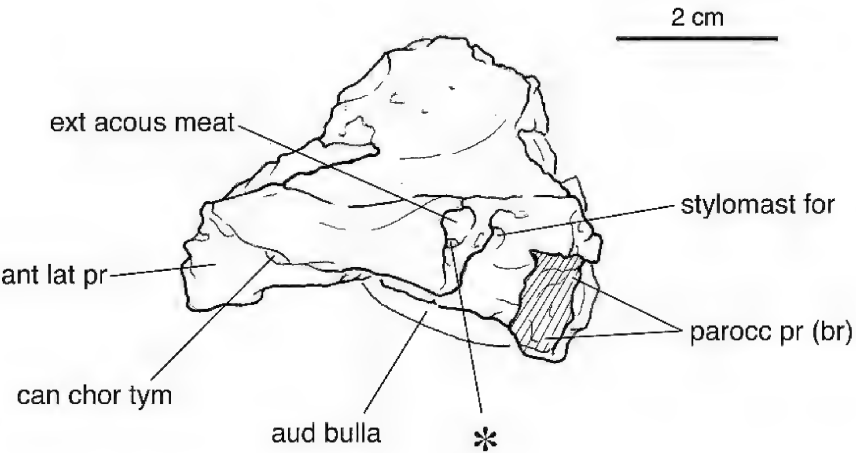


Fig. 5. *Continued.*

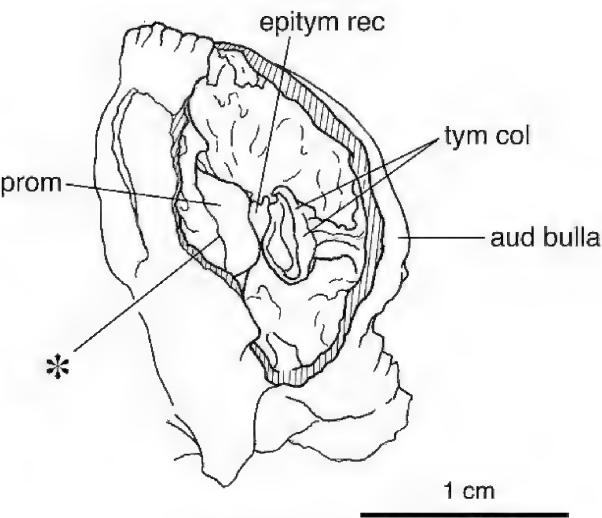


Fig. 6. *Continued.*

roof to terminate in a foramen situated on the anterosuperior side of the bulla, in front of the external acoustic canal (figs. 2, 4, 5). Judging from conditions in osteological preparations of extant caviomorphs in which dried remnants of vessels and nerves exist in this position, the tube and its aperture most likely represent the canaliculus chordae tympani. However, it is relatively large to be carrying the nerve alone, and may have transmitted blood vessels as well.

The homology of the third tube, the posttympanic canal (fig. 1), is more difficult to determine. Morphological evidence is consistent with the proposition that the canal was occupied by an artery, the ramus posttympanicus of this paper. In *Amblyrhiza* the canal runs across the posterior part of the tympanic cavity in close relation to the posterior aspect of the tympanic collar—indeed, in AAHS 95044 it appears to simply be a larger version of one of the partial septa ornamenting the latter (fig. 1). It differs, however, in that it connects with an external foramen and, instead of terminating on the collar's rim, continues onto the crest behind the posterior pole of the cochlea, where the fossula fenestrae cochleae and stapedius fossa are located (fig. 1). Under high magnification, the trace of what appears to be a small sulcus can be seen leaving the canal to run into the last-named space. The groove's course (if any) thereafter could not be determined. Externally, the canal connects with its foramen on a prominence located low on the lateral bullar wall, between and slightly ventral to the stylomastoid foramen and tympanic fenestra. Conditions are similar in AMNHVP 11842, except that the posttympanic canal is relatively shorter (and unfortunately harder to see in ventral aspect).

BASICRANIAL MORPHOLOGY OF *ELASMODONTOMYS OBLIQUUS*

The AMNHVP collection contains five partial or complete auditory regions of *Elasmodontomys*. Two are still in position on skulls: AMNHVP 14171 (holotype), from Toraño Cave near Utuado (see Anthony, 1918), badly battered but retaining the left auditory region; and AMNHVP 143605, from an unidentified cave in southwestern

Puerto Rico, in much better condition (figs. 6–7). The three remaining specimens are isolated tympanopetrosals collected by Anthony in 1916 but never catalogued prior to this study: AMNHVP 143606 (right side), from Toraño Cave, retaining an intact bulla; AMNHVP 143607 (left side), also from Toraño Cave, bulla broken; and AMNHVP 143608 (left side), locality unknown, bulla broken. AMNHVP 143607 is illustrated in figure 8. The condition of the other two tympanopetrosals is such that they do not warrant illustration or detailed description, but they were of some use in identifying certain features found on better-preserved material. Anthony (1918) collected and figured several other skulls retaining auditory regions, but unfortunately these are no longer in the AMNHVP collections.

The auditory bulla of adult *Elasmodontomys* differs from that of *Amblyrhiza* in several significant respects. It is a simple, bean-shaped excrescence, comparatively small in relation to skull size (fig. 7A), with a highly irregular external surface somewhat reminiscent of that of extant *Cuniculus*. The anterior end of the bulla is considerably roughened for reception of the medial wing of the pterygoid. As in *Amblyrhiza*, there is no indication that the external meatal margin bore accessory bones. There are many pinhole-sized foramina distributed over the bullar surface, but nothing corresponding to the large posttympanic foramen of *Amblyrhiza*.

The external acoustic canal has a complete ventral lip, with no evidence of the earlier presence of a tympanic fenestra. A vaguely defined groove on the external bullar wall runs subvertically below the external acoustic meatus (asterisk, fig. 7C). Close study of the walls of the groove indicates that it is punctuated by small foramina, but there is no indication that it was originally a gap. The deep fossa that indents the external wall of the recessus meatus in *Amblyrhiza* is also absent. Instead, this area has the same contour as the rest of the lateral bullar wall, as in other extant caviomorphs lacking the tympanic fenestra.

Other foraminal content and positioning is similar in the two West Indian taxa, as would be expected given the lack of variability in

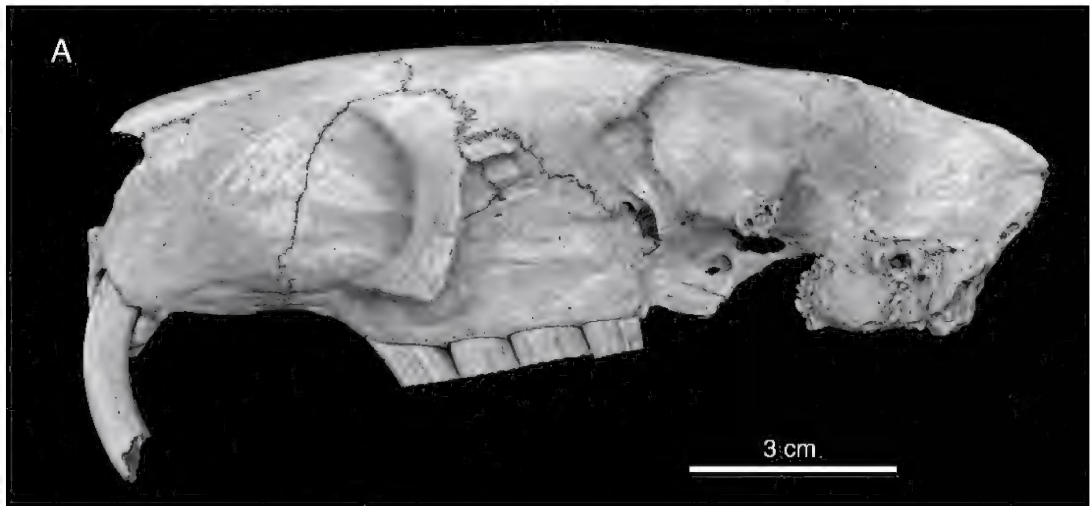


Fig. 7. *Elasmodontomys obliquus* AMNHVP 143605. A, left lateral aspect of complete skull.

such features in caviomorphs generally. The stylomastoid foramen is located below and behind the meatal aperture; a deep sulcus for the facial nerve slopes ventrally away from this foramen. The cochlear canaliculus is perched on the lip of the jugular fossa, but the aperture of entry for the tympanic nerve cannot be identified. (There are two shallow grooves on the promontorium, one of which is directed into the aperture for the tubal canal, but neither can be traced back to the posterior pole.)

The auditory region is relatively less inflated than in *Amblyrhiza*, although there are small paratympanic spaces emanating from the epitympanic recess that pneumatize the posterior and superior portions of the petrosal. The bullar wall is exceptionally thick and internally vesiculated. There are no noteworthy differences in promontorial position or shape, although in *Elasmodontomys* the line of ectotympano-petrosal contact on the ventral surface of the promontory is clearly apparent, more so than in *Amblyrhiza* (fig. 6). Apertures or grooves for the auditory tube and tensor tympani muscle are situated in the expected places (fig. 8). A large exit foramen for the chorda tympani can be detected on the outer sidewall of the bulla, but no tube for it was visible internally. The function of the aperture identified as a “venous foramen” in figure 7B and C is in

fact unknown, but as it does not conduct anything into the tympanic cavity it cannot be a posttympanic foramen. Unsurprisingly, in view of the lack of an identifiable posttympanic foramen, there is no canal running from the lateral bullar wall along the posterior aspect of the tympanic collar in any specimen. The ramus posttympanicus is therefore considered absent (figs. 6, 8).

BASICRANIAL MORPHOLOGY OF *EUMEGAMYS PARANENSIS*

MLP 41.XII.13.237 (fig. 9) is a relatively complete, albeit shattered, skull collected in 1941 by E.D. Sors in prov. Entre Ríos. The posterior cranium is in good condition, but the more anterior portions of the skull are not. The palate and much of the nasal rostrum survive as a separate piece, but the orbital, jugal, and pterygoid regions are either missing or represented by detached fragments (mandibular fossae of the squamosal, right nasal, and pieces of the right and left premaxillae).

At some point after the discovery of this specimen the floor of the left auditory bulla was carefully sawn off, exposing the middle ear cavity on that side (fig. 10). This piece could not be found when the skull was made available for study, and it is presumed lost. The sawcut was made in such a way that the external acoustic canal was transected along

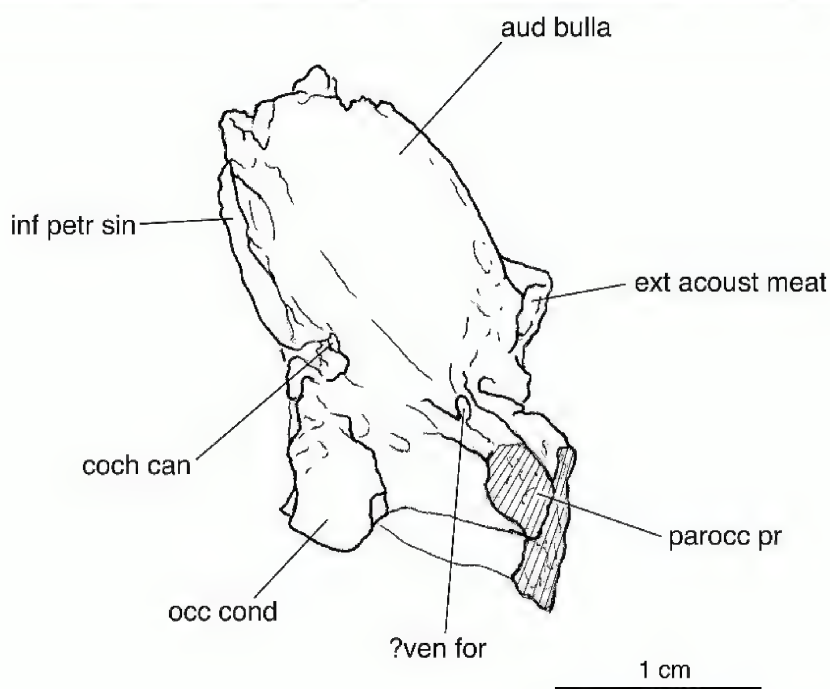
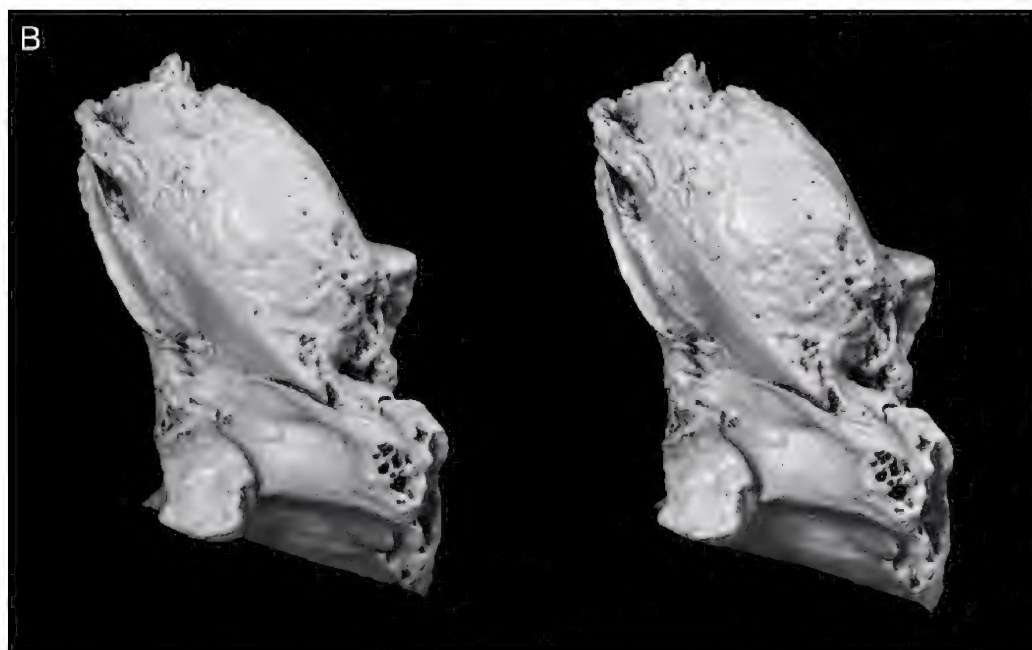


Fig. 7. *Continued.* *Elasmodontomys obliquus* AMNHVP 143605. Stereopairs (with keys) of left auditory region on this and succeeding pages: **B**, ventral, and **C** (next page), lateral aspects. Asterisk, groove on lateral bullar wall.

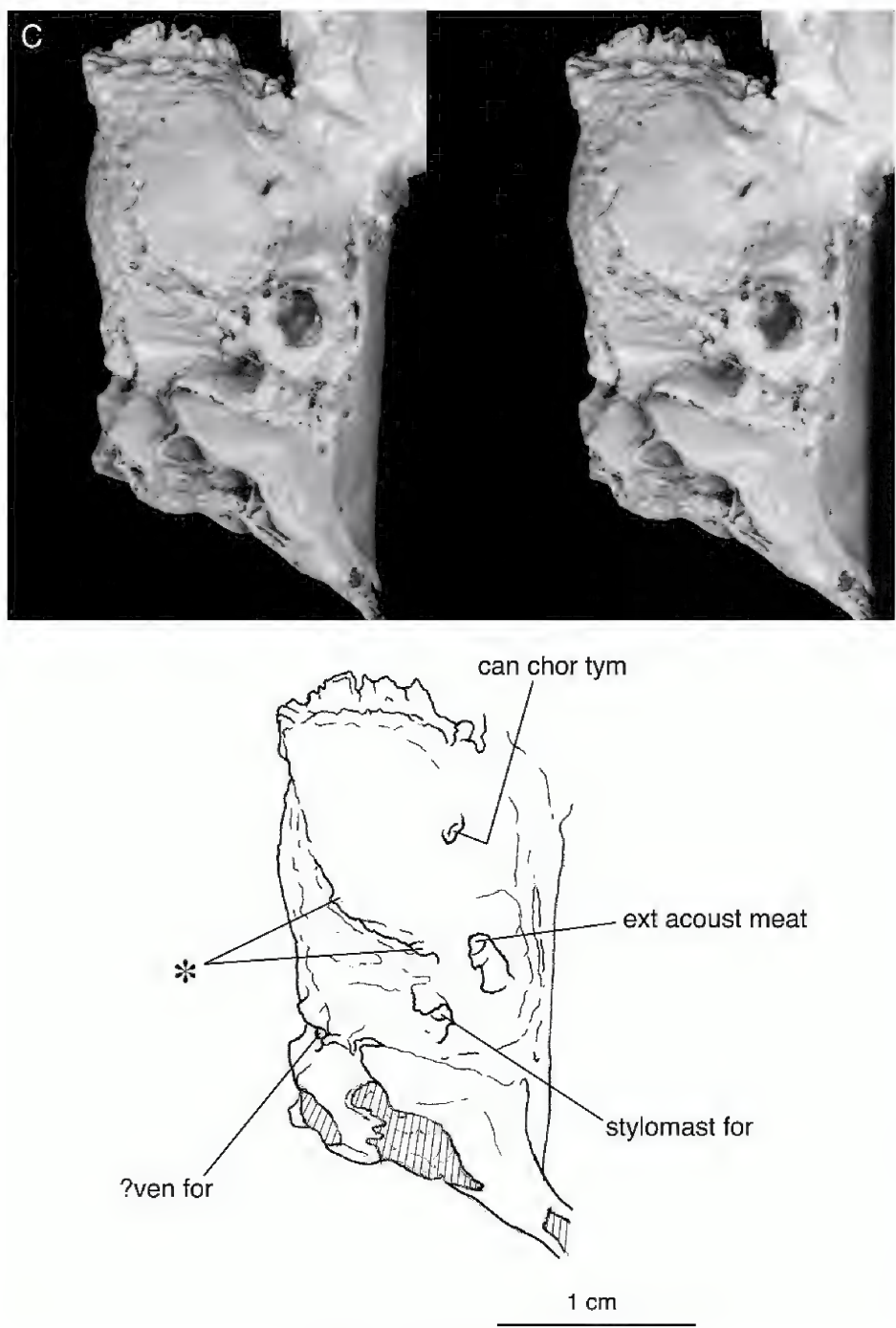


Fig. 7. Continued.

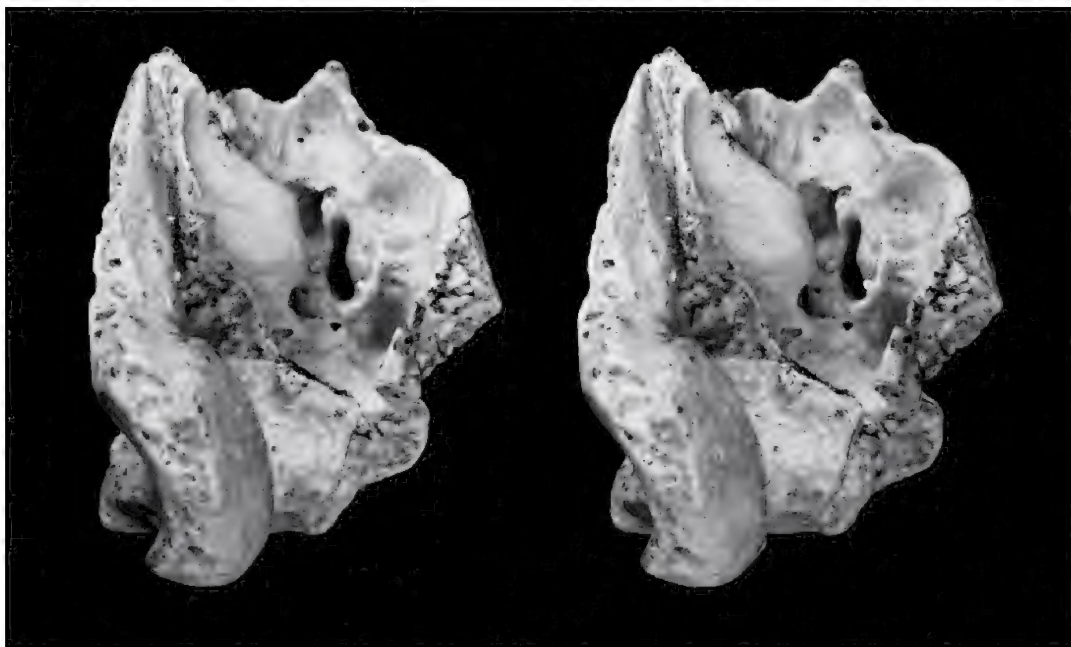


Fig. 8. *Elasmodontomys obliquus* AMNHVP 143607, left auditory region; stereopair view (with key, opposite page) in ventromedial aspect. Single asterisk identifies position of parallel grooves for auditory tube and tensor tympani muscle; double asterisks, intratympanic opening of external acoustic canal.

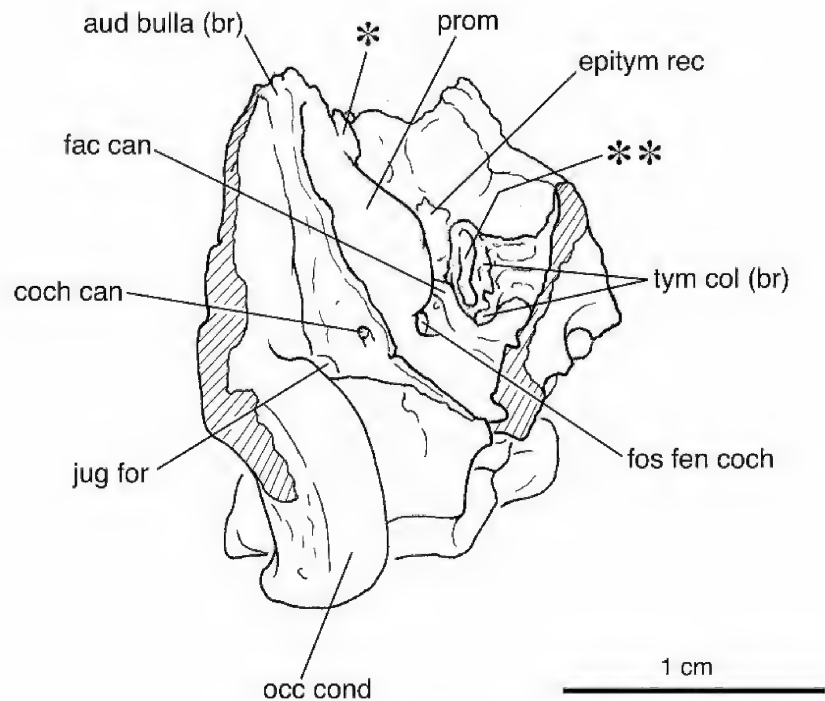


Fig. 8. *Continued.*

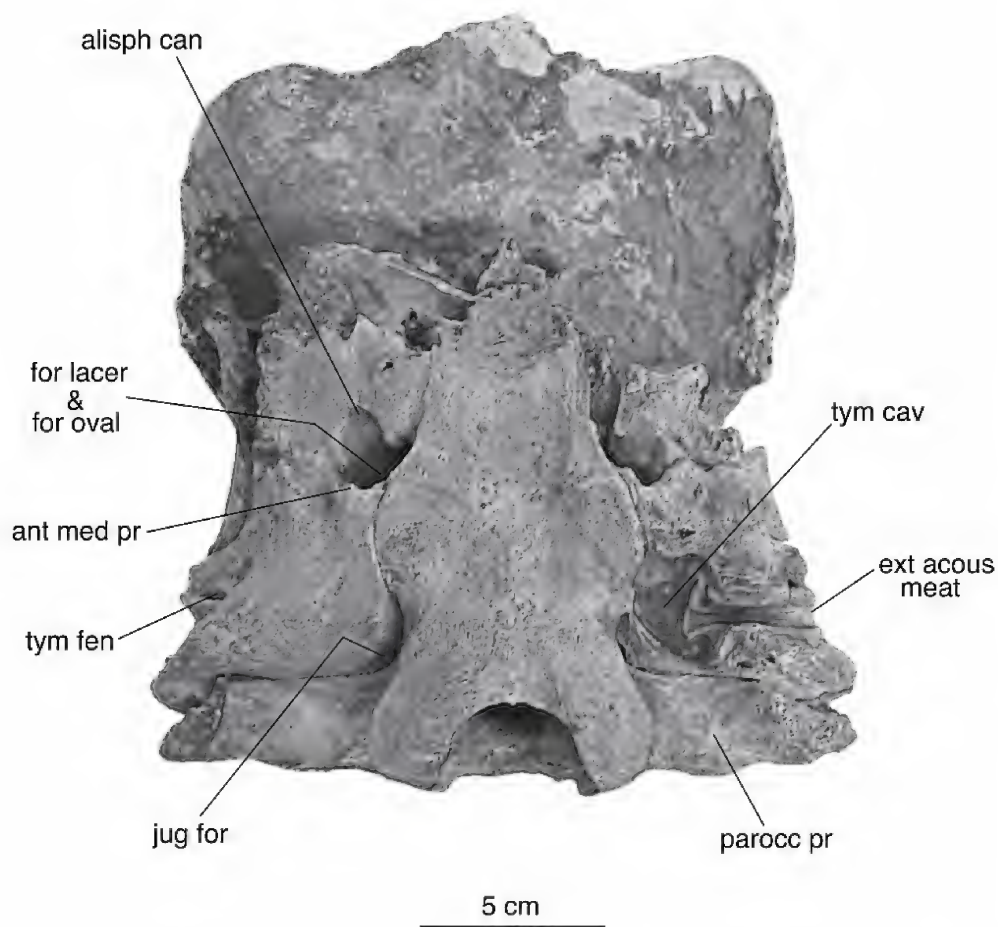


Fig. 9. *Eumegamys paranensis* MLP 41.XII.13.237, ventral view of posterior part of skull (author's photograph). Sawcut (see text) passed horizontally through the left auditory region at the level of the external acoustic canal and stylomastoid foramen. On specimen's right side, note relatively enormous foramen ovale + foramen lacerum, deep cleft in external acoustic meatus related to tympanic fenestra, position of posttympanic foramen, and robustly built glenoid and mastoid areas.

its long axis, thus revealing its extraordinary length (29 mm from position of crista tympani to lateral margin of external acoustic canal). Although the saw damaged the crista tympani and ventral surface of the promontorium, the other major features of the middle ear are otherwise mostly intact. Unfortunately, a thin scale of calcium carbonate hides most structures on the tympanic roof, and what appears to be casting material blocks many of the small apertures within the middle ear. Although it is clear from the paper by Negri and Ferigolo (1999) that the ear region of *Neoepilema* is substantially similar to that of *Eumegamys*, their account lacks sufficient detail to make useful comparisons.

As in *Amblyrhiza*, the auditory bulla is large (~35 mm, long axis) and ventrally flattened. The lateral bullar wall and related areas of the basicranium are extremely thick (fig. 10). The anterior end of the bulla terminates in two large processes, also as in *Amblyrhiza*. The more medial of the two is grooved by a large, smoothly rounded and posteriorly directed channel, presumably for a large vein connected to the pterygoid venous plexus and passing out of the enormous combined foramen lacerum + foramen ovale (11 mm, maximum width). Dorsal to this feature on the caudal lip of foramen ovale, and thus not visible in figure 9, is a large aperture which presumably housed the cartilage and ostium of the tubal canal.

The auditory region is moderately pneumatized; other than the epitympanic recess, which could not be adequately explored, there are no paratympanic spaces of large size, and only a few pneumatic cellules can be seen in the vicinity of the auditory tube, posterior wall of foramen ovale, and in the mastoid and paroccipital processes (fig. 11). By contrast, portions of the skull rostral to the auditory region, although poorly preserved (and not illustrated here), were clearly very extensively inflated. Paranasal sinus expansion evidently inflated the frontal bone in such a way that it was divided into inner and outer tables, separated by a virtually continuous airspace that extended from the nasal rostrum to the position of the coronal suture. (A similar condition can be plausibly inferred for *Amblyrhiza*, despite the lack of complete skulls for this taxon.) These massive

pneumatic chambers nearly isolated the actual bone-lined brain case—a date-sized protrusion on the cranial floor connected by septa to the cranial roof. Interestingly, the pneumatized area stops abruptly along the line of frontal/parietal contact; caudal to the coronal suture the skull is massively thickened (as in the case of the mastoid) rather than pneumatized. Such extensive buttressing might be explained as an adaptation for transmission of forces through the neck region, perhaps because the upper incisors were used for powerful digging or cutting. The thickness of the frontal bone along its posterior edge is 2.1 mm, whereas the thickness of the parietals immediately caudal to frontal contact rises to 20.5 mm—thus thicker by a factor of 10.

The upwardly and outwardly projecting external acoustic canal is nearly intact on the specimen's right side and is framed by three gaps. The rostral gap (fig. 1, single asterisk), which opens into the epitympanic recess, is simply an artifact caused by damage to the bullar wall. The teardrop-shaped aperture caudal to the meatal opening is the stylomastoid foramen; the thin, somewhat damaged wall of bone (double asterisks) separating these two apertures is interpretable as derived from the unexpanded posterior crus of the ectotympanic. The remaining dehiscence, which intersects the ventral margin of the meatus, is the tympanic fenestra in the form of a narrow slit (ventral cleft). The bulbous rostral wall of the cleft has the appearance of being turned over on itself, almost in the form of a scroll, but there is no evidence that it represents a separate ossification. In life the tympanic fenestra and the aperture of the external acoustic meatus may have been externally separated by the same damaged sheet of bone just mentioned, much as appears to be the case in the specimen of *Neoepilema* described by Negri and Ferigolo (1999), who, however, did not distinguish the fenestra from the meatus. Hypoglossal, jugular, and other constant foramina can be identified in their expected positions.

Approximately 15 mm ventral to the stylomastoid foramen there is another foramen, situated in the floor of a narrow but prominent groove (fig. 11). The foramen occupies a position similar to the posttympanic foramen



Fig. 10. *Eumegamys paranensis* MLP 41.XII.13.237, morphology of dissected ear region on specimen's left side. Photograph by author (A) was used as a basis for artist's reconstruction (B), with additional detail added after microscopic study. Unfortunately, remnant matrix hides much of the detail on the tympanic roof. Single asterisk, possible but unconfirmed portion of channel for ramus posttympanicus. Double asterisks, intratympanic rim of ectotympanic bulla overriding petrosal (promontorium).

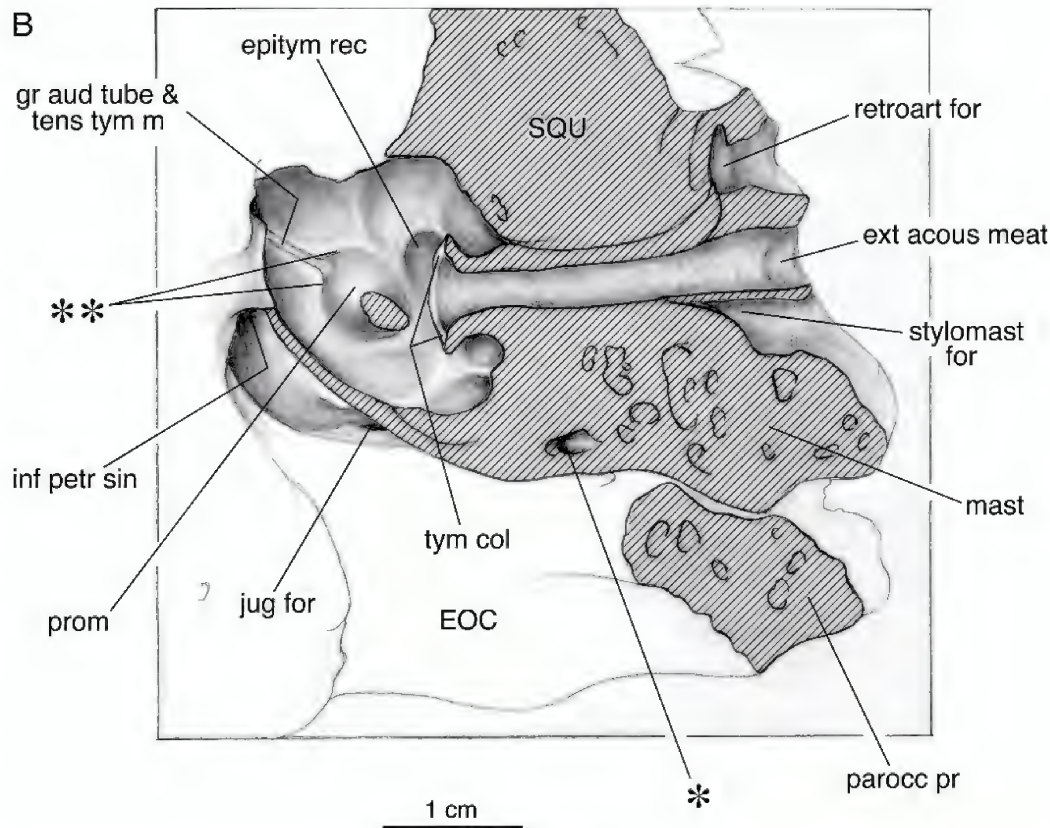


Fig. 10. *Continued.*

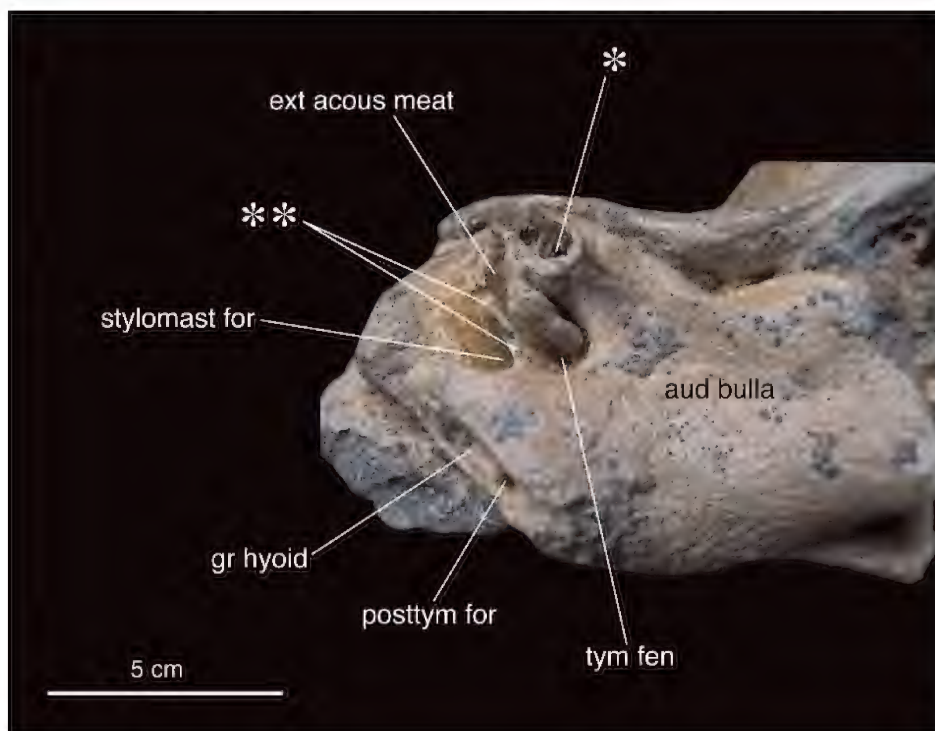


Fig. 11. *Eumegamys paranensis* MLP 41.XII.13.237, lateral aspect of right auditory region, showing external acoustic meatus, tympanic fenestra, and posttympanic foramen (author's photograph). Single asterisk, damaged lateral wall exposing epitympanic recess; double asterisks, broken wall between stylomastoid foramen and external acoustic meatus. Although the ventral cleft between the fenestra and meatus proper is continuous in this specimen, there are signs of damage here as well. It is probable that a small flange of bone, no longer present, separated the two in life (cf. comparable conditions in *Neoepilema*; Negri and Ferigolo, 1999: fig. 14).

of *Amblyrhiza*, and will be identified as such in the rest of this paper. (*Neoepiblema* apparently exhibits both apertures as well, although as previously noted Negri and Ferigolo [1999: fig. 14] assumed that both conducted parts of the facial nerve.) The identity of the groove is uncertain, although an obvious possibility is that it may have accommodated the cranial part of the hyoid apparatus, as did the similarly-situated feature in *Amblyrhiza*.

Structures on the left tympanic roof of this specimen can be studied with ease, thanks to the removal of the tympanic floor, but because of damage some points of morphological interest cannot be adequately investigated (fig. 10). This applies, for instance, to the identity of the posttympanic canal (see below). Medially and laterally the slight bulge of the promontorium is bordered by low eminences and diverticula. Some of these structures may be canals conducting nerves or arteries, but others are simply partial bony septa. The continuous ridge that borders the medial, rostral and part of the lateral side of the low promontorium appears to represent a sutural contact between the overlapping ectotympanic bulla and portions of the petrosal (promontorium + ?medial portion of the tegmen tympani) rather than a canal. Anteromedially the line of this ridge is continued forward by the low crest that divides the fossa for the tegmen tympani from the tubal canal. The area of the posterior pole of the cochlear promontorium is broken and matrix-filled, and the fenestra cochleae and vestibuli cannot be distinguished as such.

Laterally there are deep pockets in the tympanic roof surrounding the tympanic collar. The rostralmost conforms to the entrance to the greatly expanded epitympanic recess. Pockets in the rear wall of the tympanic cavity may represent the aditus of the mastoid cavity, although as already noted the mastoid part of the petrosal is itself little inflated.

Given the likely pathway of the posttympanic ramus, I have inferred that one of the apertures seen on the cut portion of the mastoid represents the posttympanic canal (here completely encased in thick bone and thus not at all canal-like). However, this is far from definite as it was not possible to pass a probe through the

aperture into the tympanic cavity (hence C3 is scored as “?” in appendix 2).

There are several subsidiary crests on the rostralmost part of the tympanic roof that can only be seen by strongly tilting the specimen (not illustrated). Most are partial septa, probably imperforate, although one prominent ridge that extends from the facial canal and bends rostromedially toward foramen ovale might have contained the lesser petrosal nerve. A less likely, but not irrelevant, possibility is that some of these crests conducted rostrally directed remnants of the stapedia system (see Development, Homology, and Character Analysis). There is no information on the middle ear cavity of *Neoepiblema*.

BASICRANIAL MORPHOLOGY OF *DINOMYS BRANICKII*

Pacarana specimens available for this study display a large aperture on the posterolateral bullar wall, situated ventromedial to the stylomastoid foramen and in essentially the same relative position as the posttympanic foramen of *Amblyrhiza* and *Eumegamys* (figs. 12–14). To confirm homology, the bulla of *Dinomys branickii* AMNHM 46551 (fig. 13A) was opened and inspected. As previously noted, in this specimen a large tube, continuous with the foramen, projects from the posterior wall of the tympanic cavity and runs thence onto the caudal tympanic process of the petrosal, where it ends, just as in *Amblyrhiza*. The end of the tube is perforated; a tiny channel issues from it and disappears into the fossula fenestrae cochleae. However, it should be noted that a complete canal is evidently not always present; in AMNHM 70354 (fig. 13B), a large adult, the posttympanic foramen opens onto a shallow sulcus on a low septum rather than a tube.

To conclusively determine the source and nature of structures traveling within the posttympanic foramen of *Dinomys*, an alcohol-preserved specimen (AMNHM 201638) was selected for detailed study. After removal from the body, the head was partly skinned and both parotid regions dissected; only the right-hand side is depicted here (fig. 14). In order to provide a window of a size sufficient to visualize relevant basicranial structures, the

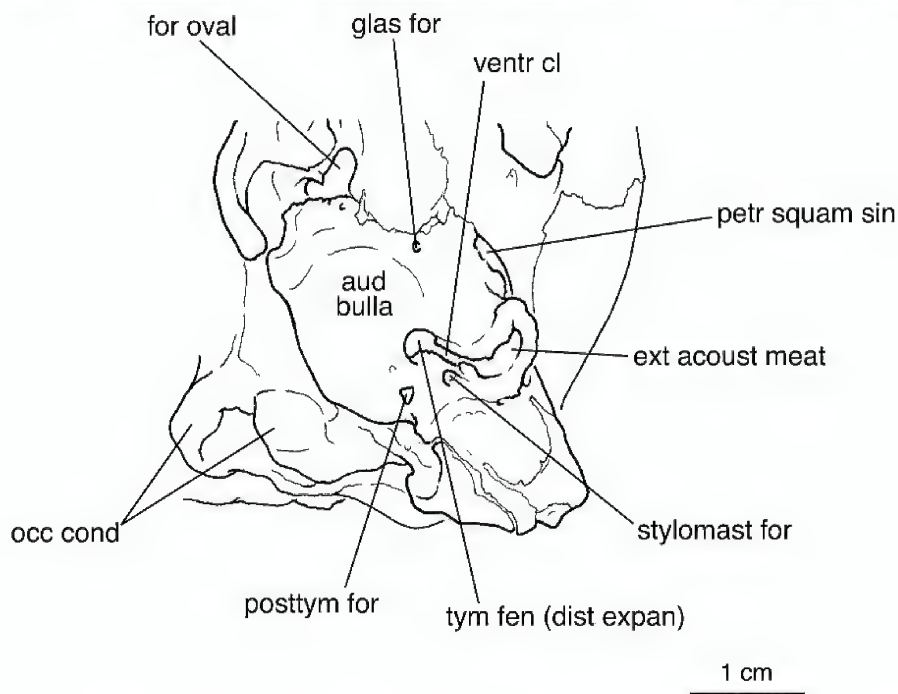
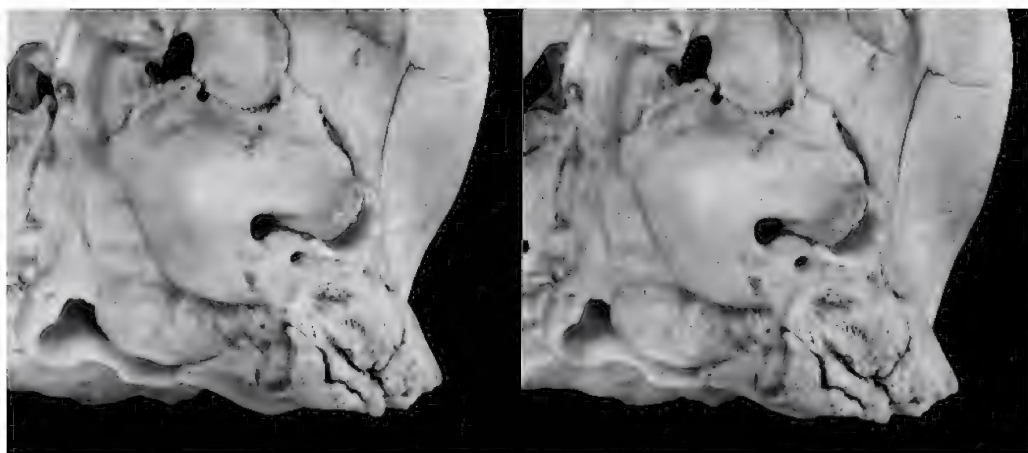


Fig. 12. *Dinomys branickii* AMNHM 185372, left auditory region; stereopair view (with key) in oblique posterolateral aspect. Visible are ventral cleft in floor of meatus and distal expansion of tympanic fenestra, as well as position of foramen for ramus posttympanicus.

gonial portion of the mandible was sacrificed, together with muscles and veins overlying part or all of the area of interest (platysma, sternocleidomastoideus, superficial masseter, pterygoid muscles; portions of the external jugular and facial veins). The digastric (both bellies) and stylohyoid (jugulohyoid) muscles were exposed but left intact. Proximal parts of the external carotid artery, internal jugular vein, and vagus nerve within the upper neck were cleaned to the point where they passed deep to the digastric. The tough meatal tissues were carefully pruned to expose the extracranial track of the facial nerve and the structures related to the posttympanic foramen, but given the delicacy of the latter it was decided not to attempt to clear the bony meatus or tympanic fenestra. Divisions of the external carotid artery were briefly followed: lingual and facial arteries were identified, but not traced rostrally beyond the parotid region, and the occipital artery (not illustrated) was found deep to the caudal belly of the digastric. Areolar tissue cleanly separated the caudal digastric from the ventral bullar wall, which was therefore easily exposed.

Only one major blood vessel traverses the potential space between the bulla and the suprahyoid musculature. From its origin on the caudal aspect of the external carotid, the vessel ascends caudodorsally in close relation to the upper free edge of the stylohyoid, crosses the nerves to the latter and the caudal digastric, then continues dorsally, closely invested by tissues comprising the membranous meatus and pinna. In these relations it strongly corresponds to, and is therefore regarded as, the homolog of the posterior auricular artery of *Homo* (see also Guthrie, 1963).⁴ At least in

the area surveyed there was no evidence of a true internal carotid artery medial to the external carotid trunk, and the former is judged to be absent (either completely or at the stage represented by this specimen).

The postganglionic end of the sympathetic system is represented by a small trunk that becomes an extensive plexus on the external carotid. A separate deep petrosal nerve, like that found in primates, eulipotyphlans, and several other groups, which travels through the middle ear to the pterygoid canal where it meets the greater petrosal nerve (MacPhee, 1981), was not seen. Since the course of the internal carotid artery is extrabullar even in the one group of caviomorphs (erethizontids) known to exhibit this vessel in the adult stage (Bugge, 1974a, 1974b), postganglionic sympathetic fibers destined for the nasal mucosa, lacrimal gland, and other cranial targets must be distributed along branches of the external carotid artery and thus never pass through the middle ear.

The chief targets of the dissection were the stylomastoid foramen and posttympanic foramen. With careful cleaning of meatal tissues adherent to the posterolateral wall of the bulla, the usual branches of the facial nerve were identified as they left the stylomastoid foramen. A few millimeters posteriorly, a small division of the posterior auricular artery was seen to penetrate the bulla at a position that corresponds to the expected entry point of the ramus posttympanicus. This interpretation is fully consistent with the inferences made on the basis of osteology. In order to preserve anatomical relationships in the dissected specimen for future reference, it was decided to end the dissection leaving the bullae intact (fig. 13).

⁴Cooper and Schiller (1975: fig. 4–15) identify the stem of the apparent equivalent of this vessel in *Cavia* as the superficial temporal artery, probably because it releases a large rostral branch that appears to supply the same area as the superficial temporal in *Homo*. In their figure there is, however, an equally large (unnamed) caudal branch that appears to correspond to the posterior auricular. Whether this compound arrangement is widespread among caviomorphs is not known. However, in *Dinomys* AMNHM 201638 there is only the caudal branch. Although the point was not checked during dissection, the equivalent of the superficial temporal must originate separately, presumably from the maxillary artery. Cooper and Schiller also depict a twig of their rostral branch penetrating the bulla of *Cavia* beneath the ventral lip of the meatus—a meatal innominate vessel in the terminology of the present paper.

RELEVANT BASICRANIAL FEATURES OF EXTANT CTENOHYSTRICAN FAMILIES

In character definition and analysis it is important to be able to distinguish between structures that appear to be operationally homologous from those that are not. The purpose of this section is to briefly summarize, for comparative purposes, relevant developmental and morphological aspects of the basicrania of crown-group Ctenohystrica, with an emphasis

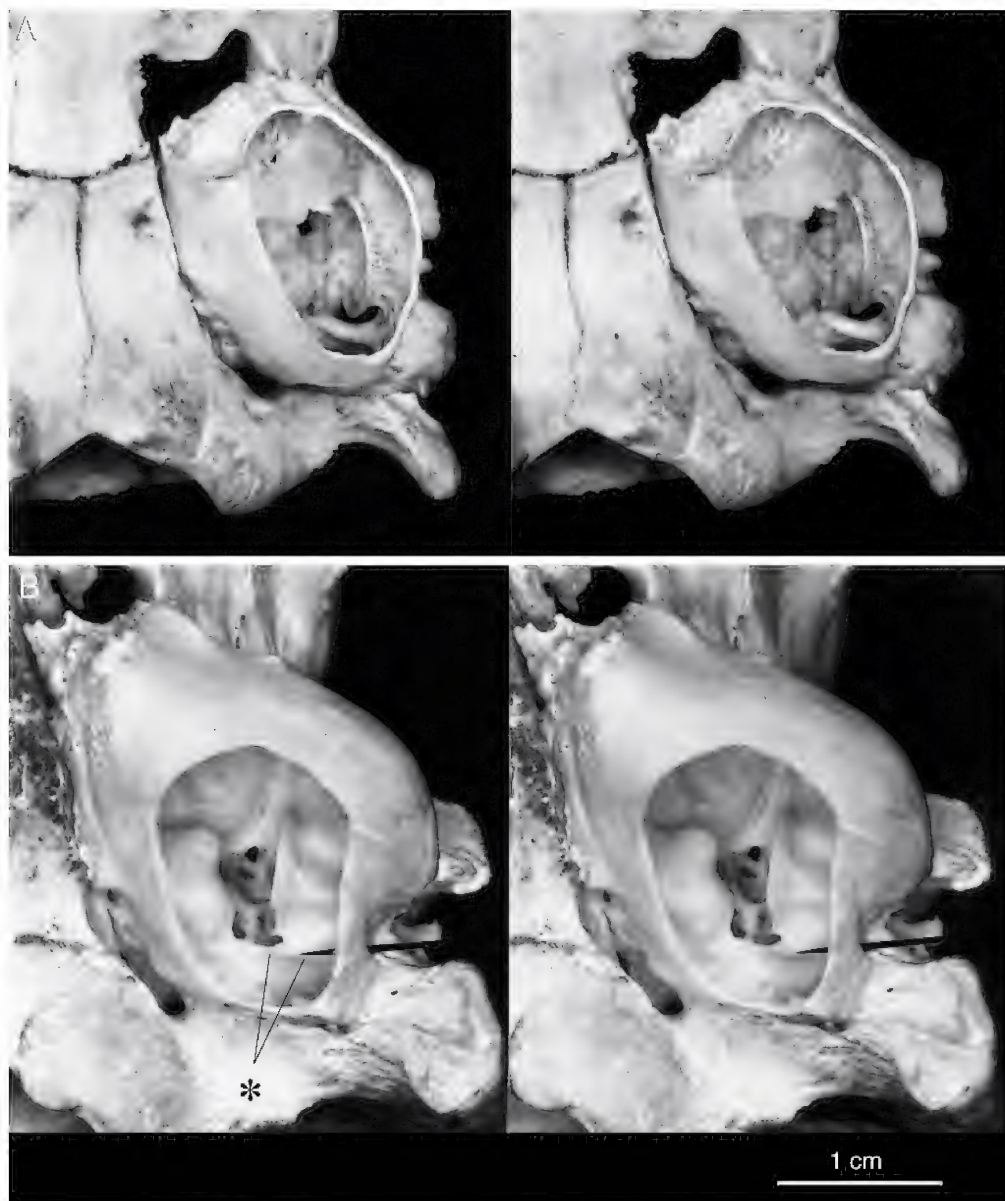


Fig. 13. *Dinomys branickii* AMNHM 46551 (A); and AMNHM 70354 (B), right auditory regions (rev.), stereopair views (with key for A) in oblique ventral aspect. In A, the bullar floor and ossicles have been removed to expose the posttympanic canal; the facial canal lies more dorsally and thus is not visible. Because of the viewing angle, the posttympanic foramen, tympanic fenestra, and external acoustic meatus (asterisk and arrows) are hidden by the bullar wall. In the second specimen (B), the posttympanic ramus (suggested by pin) was conducted into the tympanic cavity along a partial septum (asterisk) rather than through a canal. The difference is not due to ontogenetic age, as AMNH 46551 is a juvenile in which cranial sutures are still widely open while AMNHM 70354 is fully adult. (The third pacarana available for osteological study, AMNHM 185372, exhibits large, possibly pathogenic exostoses in its tympanic cavity and presence of a canal could not be determined.)

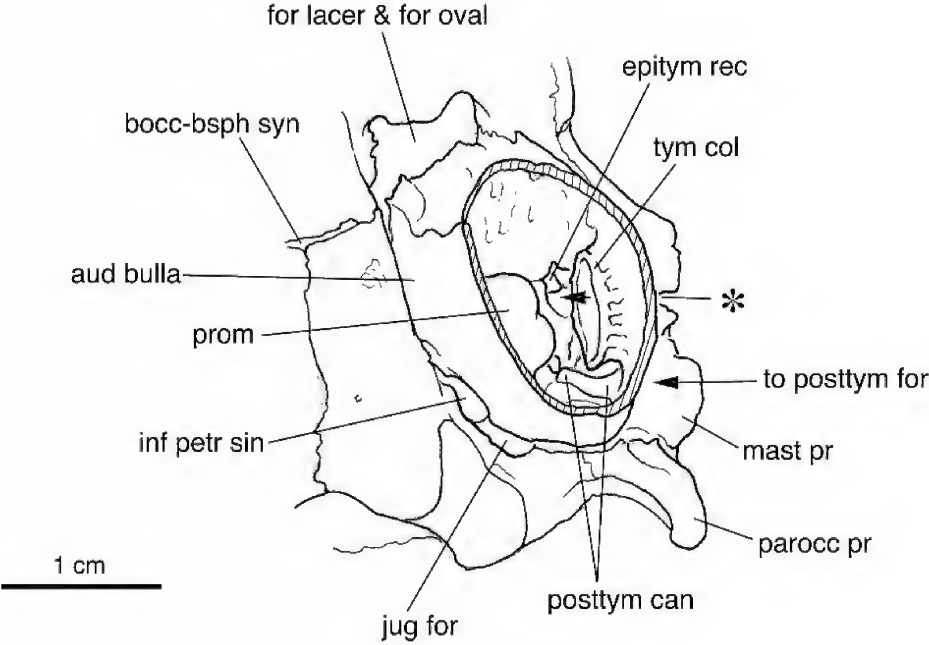


Fig. 13. *Continued.*

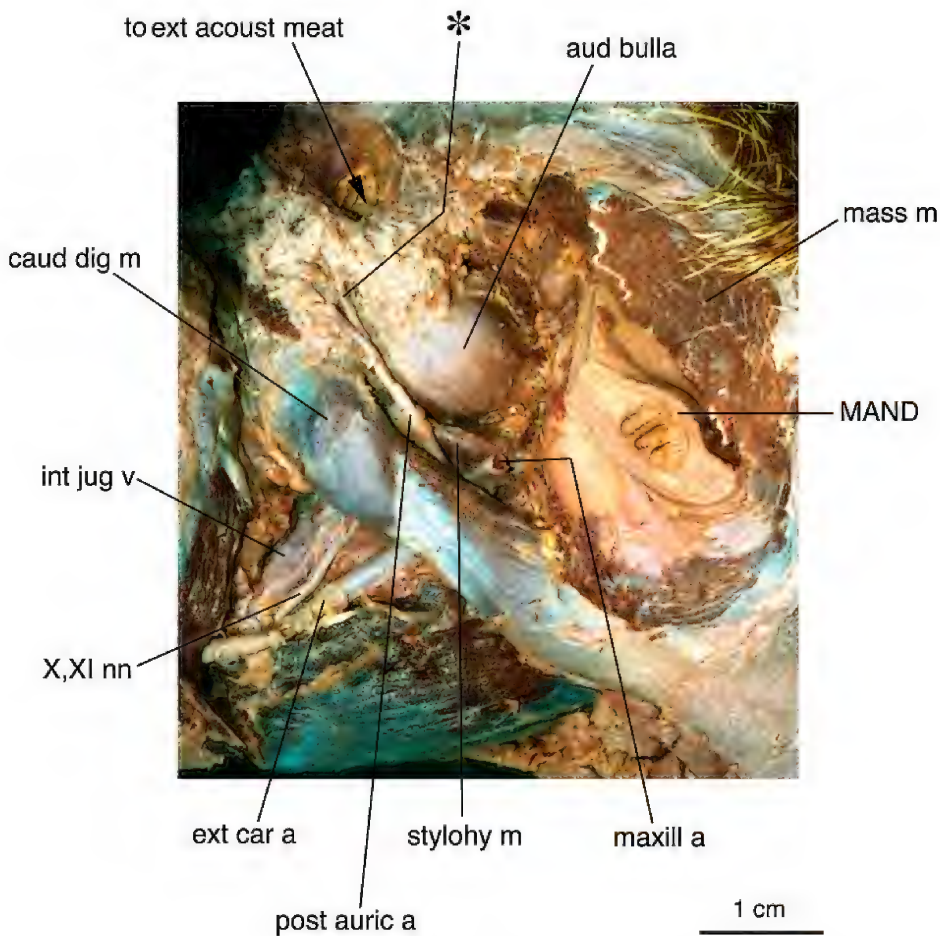


Fig. 14. *Dinomys branickii* AMNHM 201638; dissection of right side, oblique ventrolateral aspect. Structures superficial to the plane of the caudal belly of the digastric, including the gonial portion of the mandible, have been transected or removed to provide an unimpeded view of the auditory bulla and route of the superficial temporal/posterior auricular artery. (In the case of the mandible, cut extended into molar roots, as is evident here.) Tough meatal tissues occlude the tympanic fenestra; these were left in place so as not to damage the branch (asterisk) that gives off the ramus posttympanicus.

on caviomorphs. Except for the main targets of this paper, extinct taxa are usually not referenced. Their study is well beyond my immediate purpose, and, in any case, there are virtually no paleontological studies with much relevance to the points of interest here. Although conditions in at least one member of each extant family (as recognized by Woods and Kilpatrick, 2005) are described, only a subset of these could be illustrated photographically. These are, however, augmented by short descriptions of particular specimens in the AMNHM and USNMM collections.

Ctenodactyloidea

Ctenodactylidae: In *Ctenodactylus gundi* USNMM 325852 (fig. 15) there are at least six meatal innominate foramina punctuating the lateral bullar wall along the outer curve of the crista tympani—a ctenohystrican maximum. There is no posttympanic foramen evident externally and no canal internally. The lateral wall is complete, with a lengthy external acoustic canal, and there is no indication that a tympanic fenestra was transitorily present earlier in ontogeny. The pessulus is present in this specimen.

Phiomorpha

Although tiny foramina occur in the circummeatal area in phiomorphs (figs. 16–18), the only constant, sizeable aperture on the lateral bullar wall is the stylomastoid foramen. However, notice should be made of a large external groove (sometimes taking the form of a partly bridged canal) situated behind the posterior margin of the meatus in the available specimens of *Bathyergus*, *Hystrix*, *Atherurus*, and *Thryonomys* (but not *Petromus*). A similar feature is seen in many caviomorphs, suggesting that it is probably primitive for hystricognaths. The vessel occupying the groove is assumed to be homologous with the posterior auricular artery, which in placentals typically ascends behind the meatal opening to feed the external ear and related portions of the scalp. Given the generally close proximity of the stylomastoid foramen to the artery's trackway, it is not unlikely that it releases small branches to the former in

order to feed local structures. However, none of these taxa displayed features conforming to the posttympanic foramen or canal as seen in *Dinomys*. If the equivalent of the ramus posttympanicus exists in these taxa, it must travel to its targets via the facial canal (rather than through an independent tube), and is thus not detectable osteologically.

Diatomyidae: The basicranial morphology of the only extant member of this formerly widespread family, *Laonastes aenigmamus* (see Jenkins et al., 2005), has not yet been described in detail and a specimen was not available for the present study. However, it is obvious from drawings and photographs (see also Dawson et al., 2006) that the Laotian rock rat lacks a tympanic fenestra and perhaps foramina for meatal innominate vessels in the adult stage. The external acoustic meatus is described as “tubular, with a shallow posteroventral lip,” and “incomplete septa” occur within the tympanic cavity.

Bathyergidae: In *Bathyergus* the posterior portion of the petrosal is massively inflated. Although there is no sign of any remnant of the stapedia system (a pessulus is lacking in the specimens examined), there is a prominent septum, containing a tube, that passes from the middle portion of the medial bullar wall to the promontorium, well in advance of the cochlear windows. In some mammals, a septum and tube in this position might be expected to contain the internal carotid and its accompanying sympathetic nerve, but a more likely possibility for *Bathyergus* is that it contains the tympanic nerve only. The lateral bullar wall is not perforated by a fenestra.

Hystrichidae: Small nutrient foramina populate the general area of the meatus and stylomastoid foramen in different species of *Hystrix* (see fig. 16), although as in other phiomorphs none is large or associated with an intratympanic canal. The possibility that adult *Hystrix* preserves an internal carotid artery, as claimed by Tandler (1901), is reviewed in a later section. Pessulus absent.

Petromuridae: *Petromus* is the only phiomorph examined in which the tympanic fenestra (C1:1) is arguably present in the adult stage, as a notch separated from the porus meatus by a strap of bone (fig. 17). Pessuli occur, but no posttympanic foramen or canal could be identified.

Thryonomyidae: *Thryonomys swinderianus* AMNH 216340 (fig. 18) lacks a tympanic fenestra, but there is a vascular aperture immediately adjacent to the stylomastoid foramen. However, it is directed posteriorly, away from rather than toward the tympanic cavity. Furthermore, the aperture is situated on the border between petromastoid, paroccipital process, and bulla proper, which is unlike the condition in *Dinomys* in which the posttympanic foramen is positioned more rostrally, within bullar material. Thus, the aperture in question is probably a true mastoid foramen, for venous drainage of the mastoid area as also seen in many caviomorphs (see *Myocastor coypus* AMNHM 80097, fig. 22A). The stapedial pessulus is lacking in the specimens examined.

Caviomorpha Erethizontoidea

Erethizontidae: As discussed below, in adult *Erethizon dorsatum* AMNHM 20773 (fig. 19A, B) a discrete foramen occurs on the posterior wall of the bulla that is in the correct position to have conducted a ramus posttympanicus. The foramen debouches onto a grooved septum (bristle, fig. 19B) that continues onto the tympanic roof lateral to the vestibular window, where it becomes indistinct. In *Coendu mexicanus* AMNHM 204282 there is a similarly positioned foramen; whether it opens into the tympanic cavity could not be confirmed, but it seems likely that it does. Although dissection of an injected specimen would be desirable for confirmatory purposes, the circumstantial evidence is heavily in favor of the presence of the ramus (thus **C2:1**) in erethizontids. These findings are of great interest, as *Erethizon* is the only caviomorph for which developmental information exists with a bearing on the likely nature of the ramus posttympanicus (see Ramus Posttympanicus as Stapedial Ramus Posterior).

Chinchilloidea

Dinomyidae: This family is separately treated in preceding sections (see also figs. 12–14); ramus, canal (or incomplete septum), and fenestra are all present. The

pessulus was lacking in the two specimens available for detailed investigation.

Chinchillidae: *Lagostomus* (fig. 20) and *Lagidium* (not illustrated) present massively inflated bullae with complicated interiors. In adult *Lagostomus* the external acoustic meatus is drawn out into a long tube, the posterior margin of which is deeply grooved by the passage of the posterior auricular artery (cf. similar condition in phiomorphs) and, immediately adjacent to it, the stylomastoid foramen. In *Lagostomus maximus* AMNHM 246958 and 80208 a foramen perforates the medial wall of this groove, apparently directed toward the facial canal. It has the correct relations to be a conduit for the posttympanic ramus, although dissection of the left auditory region of *Lagidium viscacia* AMNHM 144954, which is broken at the position of the stylomastoid foramen, failed to reveal any sign of a vessel leaving the facial canal for the tympanic cavity. Identification is therefore provisional (**C2:2**). No posttympanic canal was detected inside the middle ear in either genus. Pessulus is present in specimens of both genera. Study of the ear region of *Chinchilla* was less satisfactory because the middle ear is even more pneumatized, with many septa of uncertain significance.

Octodontoidea

Abrocomidae: In *Abrocoma bennetti* AMNHM 33273 the middle ear is highly inflated and sculpted, with notable septal content, but there is no recognizable posttympanic foramen or canal. Pessulus is present. Chinchilla rats have sometimes been regarded as closely related to Chinchillidae (Glanz and Anderson, 1990), but molecular data clearly support positioning them within Octodontoidea (Huchon and Douzery, 2001). The basicranium shows none of the distinctive features of chinchilloids: the tympanic fenestra is absent and there are only small foramina for meatal innominate vessels, as in octodontoids generally.

Capromyidae: The posttympanic foramen could not be detected and the intratympanic canal is not present. There is no indication that a tympanic fenestra is formed early in ontogeny (fig. 21). The pessulus exists in

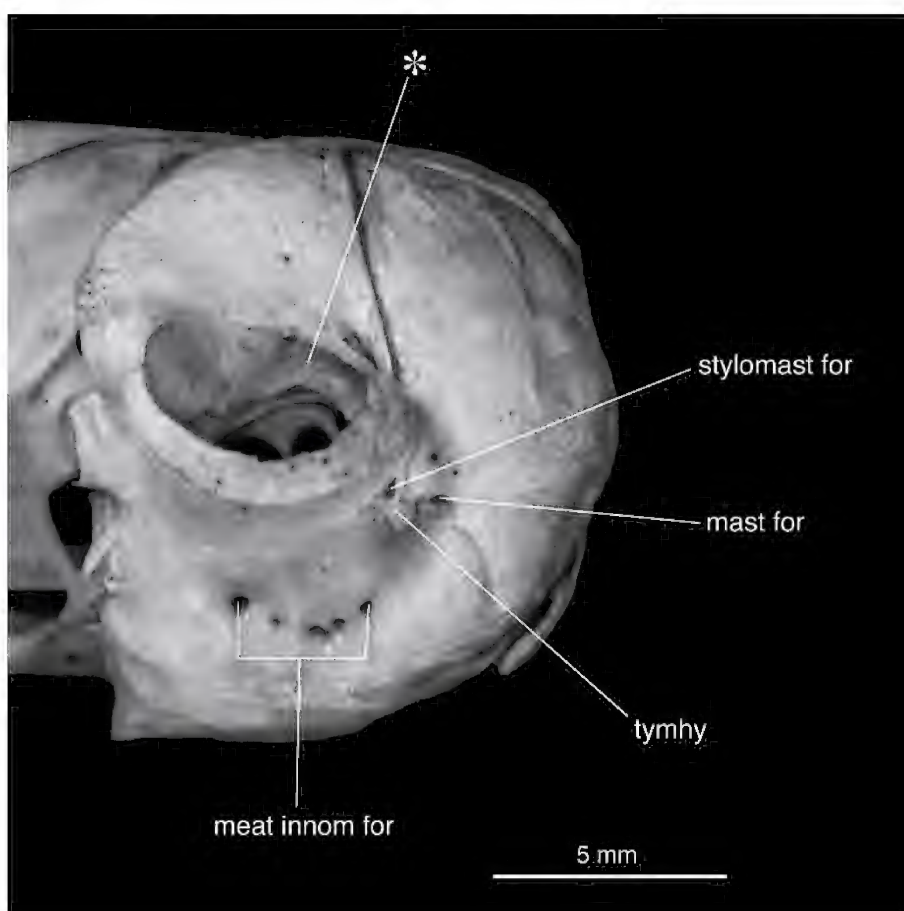


Fig. 15. *Ctenodactylus gundi* USNMM 325852, right auditory region (rev.), in ventromedial aspect. The lateral wall is intact, with many perforations for meatal innominate vessels but no tympanic fenestra or posttympanic foramen. Also partly visible in this aspect is the unusual partial septum just inside the aperture of the external acoustic meatus, which forms a kind of “secondary” meatus (asterisk). It is not the crista tympani, which is situated more medially (and not visible in this aspect).

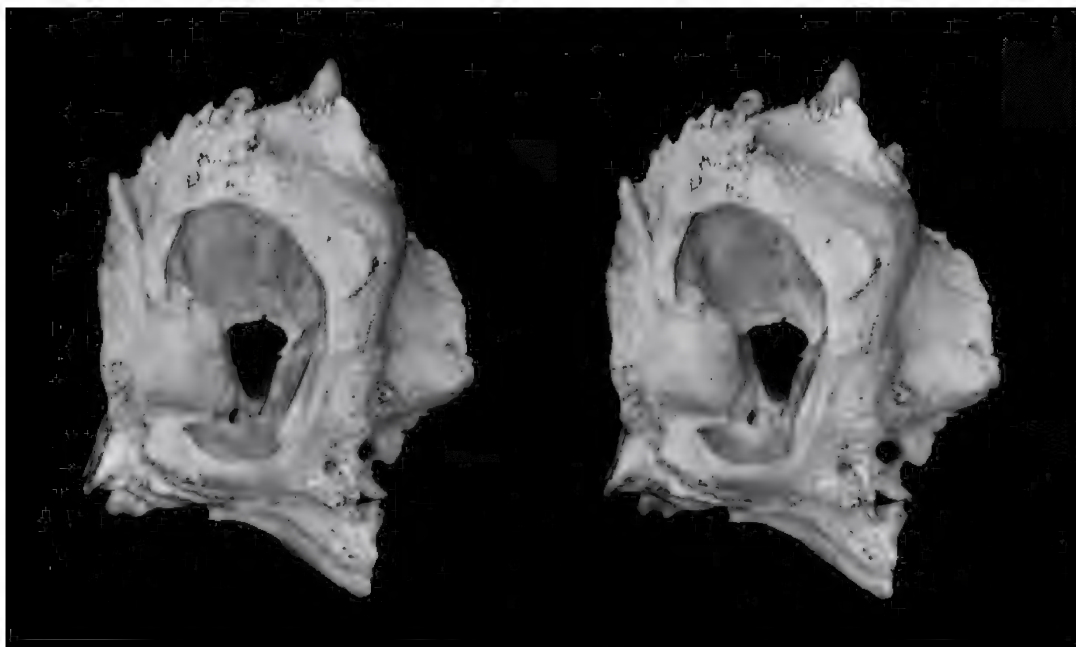


Fig. 16. *Hystrix indica* AMNHM 240917, right (rev.) tympanopetrosal; stereopair view (with key, opposite page) in ventromedial aspect. The medial wall of the bulla has been removed, including most of the portion that lapped onto the adjacent promontorium, thus exposing the ectotympano-petrosal suture in cross-section. The large aperture (double asterisks) rostral to the stylomastoid foramen passes vertically through the posterior margin of the meatal lip but does not enter the tympanic cavity. A similar feature is seen in other phiomorphs; the vessel transmitted through this foramen is presumably the posterior auricular artery. The deep pit (single asterisk) in the same area is blind, and presumably accommodated the tympanohyal in life. The sulcus on the promontorium is interpreted as part of the track of the tympanic nerve, not the internal carotid (contra Tandler, 1901).

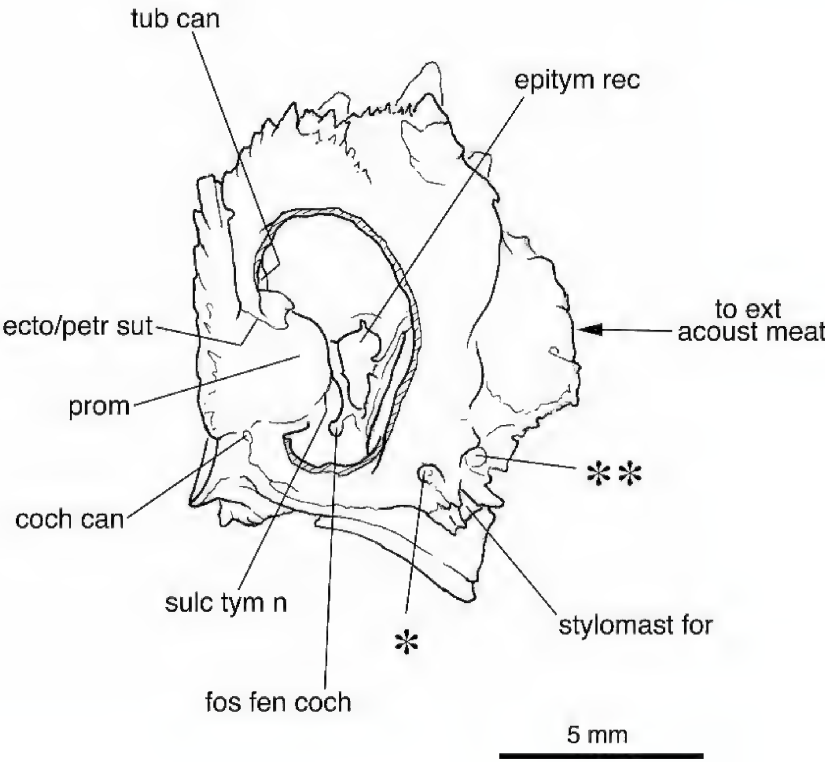


Fig. 16. *Continued.*

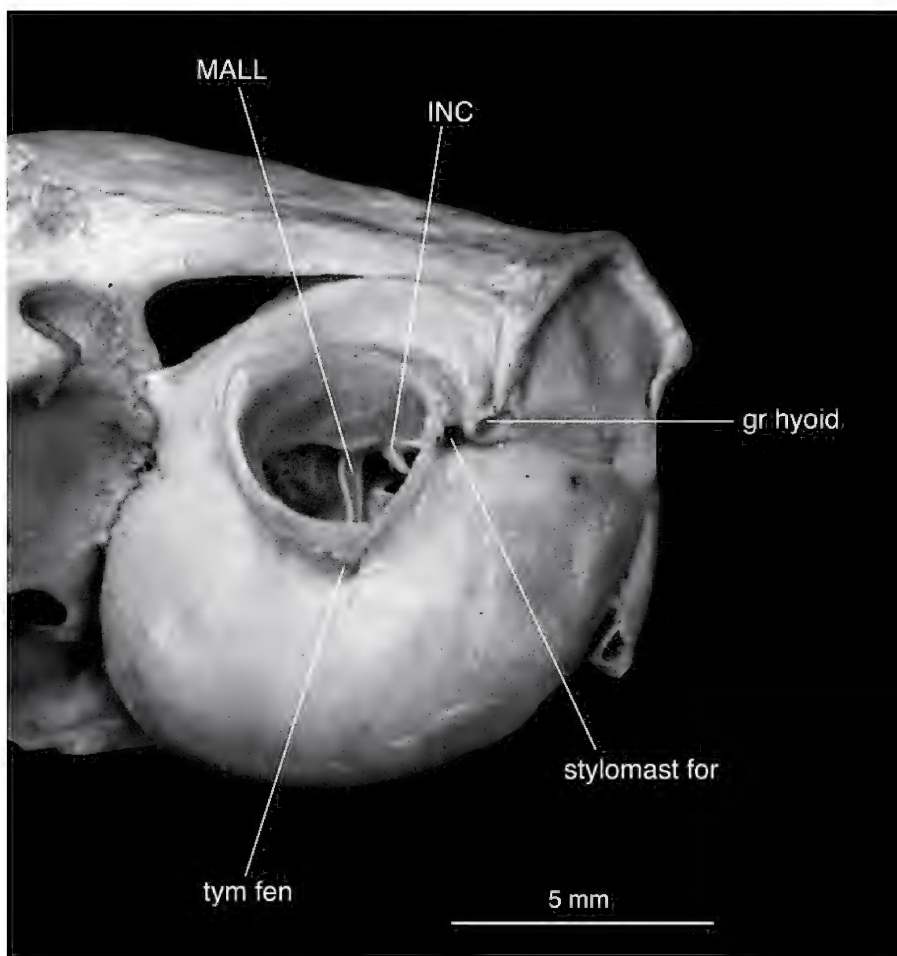


Fig. 17. *Petromus typicus* AMNHM 34393, right auditory region (rev.). Note straplike process separating the small tympanic fenestra from the meatus. The former was initially scored as a (large) foramen for meatal innominate vasculature. However, closer inspection revealed that a plug of meatal tissues was still in place, and only after pulling it away on the opposite side (not photographed) did it become evident that a notchlike tympanic fenestra (C1:2) was present, like that of some caviomorphs. In some other specimens (e.g., AMNHM 165295) the fenestra has a more complex shape, but is still scored as present.

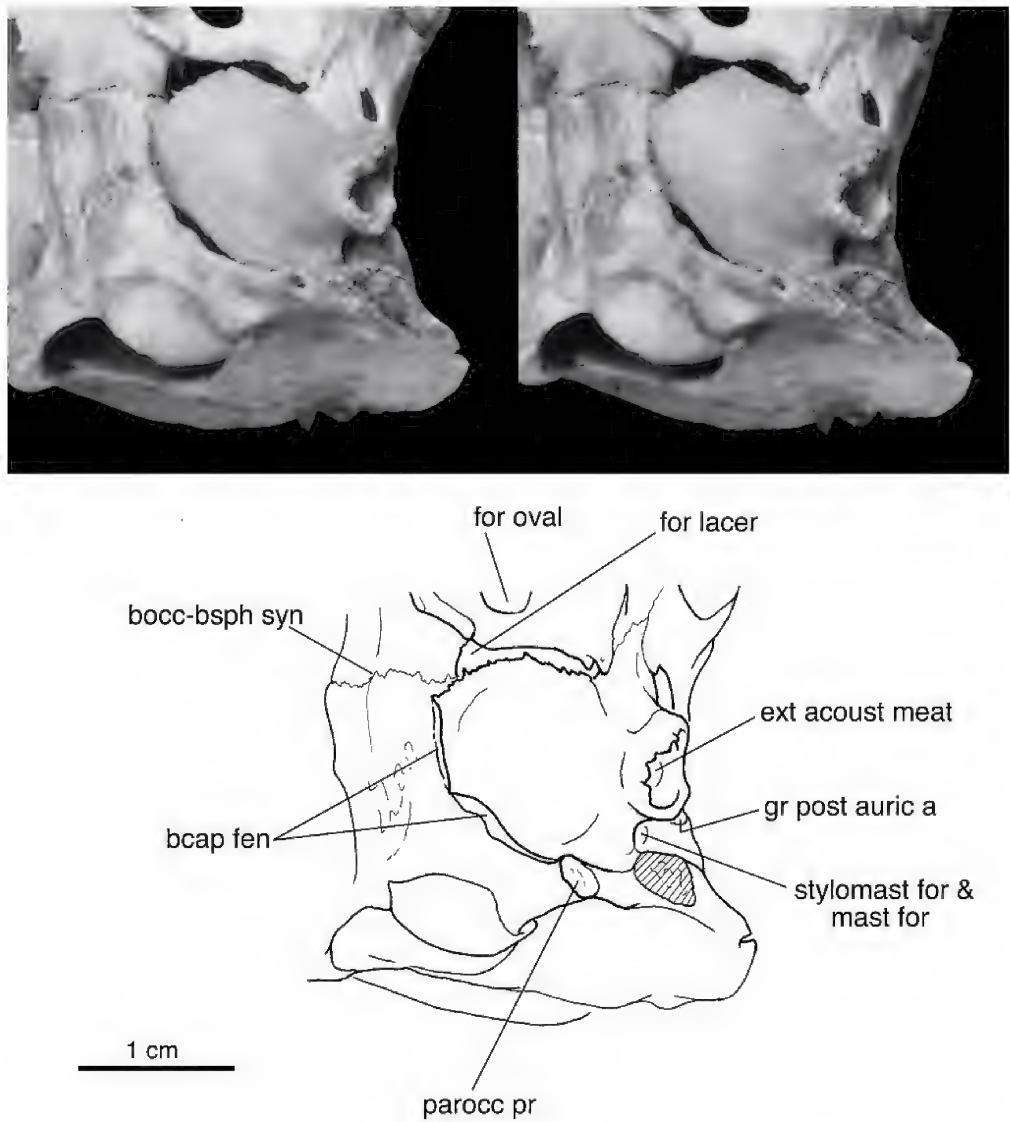


Fig. 18. *Thryonomys swinderianus* AMNHM 216340, left auditory region; stereopair view (with key) in ventrolateral aspect. Like all phiomorphs, cane rats lack an evident aperture for the posttympanic ramus (see text). The tympanic fenestra is absent as such, as are any apparent perforations for meatal innominate vessels. Hatchure indicates damage.

Geocapromys brownii AMNHM 45156. (fig. 21).

Echimyidae: This is a speciose group, but basicranial characters are relatively uniform in the four taxa investigated—the eumysopines *Proechimys guyannensis* and *Lonchothrix emiliae*, the dactylomyine *Dactylomys dactylinus*, and the echimyine *Echimys* sp. Although the bullae are primitively bean shaped in all specimens, with no posttympanic foramen and an unbreached external acoustic meatus, middle-ear pneumatization is marked, producing near isolation of the crista tympani from the lateral bullar wall in eumysopines in particular. All specimens displayed a single meatal innominate foramen under the meatal lip; the margins of the foramen were ragged, however, especially in the dactylomyines, indicating that the aperture developed by gradual enclosure. However, it is never as large as in *Octodon* (see below) and therefore the tympanic fenestra is scored as absent, although I recognize this is a judgment call. A pessulus was detectable in the dactylomyine specimens and *Proechimys guyannensis* AMNHM 92952, but was either absent or indeterminable in the other specimens.

Myocastoridae: In *Myocastor coypus* AMNHM 80097, a young animal with P1 and M1 erupted but only slightly worn, a foramen just below the lip of the right meatus leads to a sulcus on the shelflike tympanic collar. On the left side the foramen is not in evidence but the sulcus, evidently for meatal innominate vasculature, can be clearly seen (fig. 22A). The only other aperture in the area is the mastoid foramen, clearly leading into the mastoid; there is thus no foramen or tube for the ramus posttympanicus. The pessulus is present in this particular specimen, but is apparently absent on the examined (right) side in *M. coypus* AMNHM 35626. Whether there is real variability will have to be determined on the basis of a larger sample.

Octodontidae: This family, also markedly speciose, is fairly conservative for the characters under consideration. In a representative sample consisting of *Octodon degus* AMNHM 242476, *Octodontomys gliroides* AMNHM 249052, and *Spalacopus cyanus* AMNHM 33296, the posttympanic foramen and canal are lacking, but a pessulus is present in the first two. In the specimen of

Octodon the tympanic fenestra is present as a ragged-edged gash, and is scored as present (C1:1); in the others there is only a pinhole for innominate meatal vasculature.

Ctenomyidae: *Ctenomys magellanicus* AMNHM 17445 exhibits a highly inflated middle ear with elaborate septal content, like some octodontids (e.g., *Octodon*), but there is no posttympanic foramen/canal. There is, however, a pessulus and a restricted foramen for innominate vasculature (C1:0).

Caviidae: *Cavia aperea* AMNHM 264468 features a well-defined fenestra, completely walled off from the external acoustic meatus, with a distal expansion and a partially closed ventral cleft. This specimen also presents good examples of accessory bones attached to the lip of the moderately developed meatal canal. There is neither posttympanic foramen nor canal in this specimen or *Dolichotis patagonum* AMNHM 48218, but the pessulus is present in the latter, as is a fenestra similar to that of *Cavia*. *Galea musteloides* AMNH213465 exhibits the same combination of conditions. As noted elsewhere, Aihara (1958) presented a detailed dissection of middle-ear vasculature in *Cavia*, but did not address the problem of homological equivalents.

In *Hydrochoerus hydrochaeris* AMNHM 15468 (fig. 23), a young animal, there is a foramen situated immediately posterior to the stylomastoid foramen. However, probing with a bristle reveals that this foramen leads not into the tympanic cavity but instead into the open suture between the petrosal mastoid and the exoccipital (paroccipital process). It is therefore considered the mastoid foramen. The pessulus is absent, but the fenestra is well developed. The ventral cleft is quite ragged with opposing edges widely separated, as in some adult capybaras (e.g., *H. hydrochaeris* AMNHM 206444). In others (*H. hydrochaeris* AMNHM 98634 and 134102, both large adults) the spiculate edges of the cleft are actually in contact, with a slight distal expansion conforming to the tympanic fenestra. As in *Dinomys branickii* AMNHM 185372 (fig. 12), there is a long cleft formed by nearly approximating bone territories.

Dasyproctidae: The posttympanic foramen and tube are absent in *Dasyprocta punctata* AMNHM 41394 (fig. 24), a young specimen, but the tympanic fenestra is well

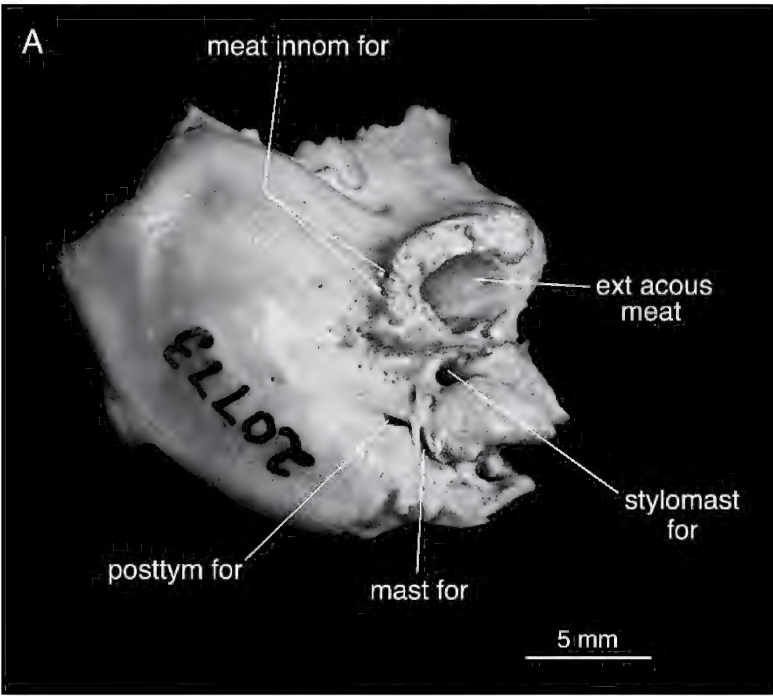


Fig. 19. *Erethizon dorsatum* AMNHM 20773, (A) left and (B) right (rev.) isolated tympanopetrosals. A, oblique lateral aspect; B, stereopair in posteroventral aspect with bullar floor removed (posterior end toward top) and key on following page. Foramen visible on posterior bullar wall in A is the posttympanic foramen, through which, in B, a bristle (single asterisk) can be passed into a hemicanal (double asterisks). Hemicanal is inferred to have carried the ramus posttympanicus. The tympanic fenestra is absent in this species, as in other erethizontids, although meatal innominate foramina are conspicuous.

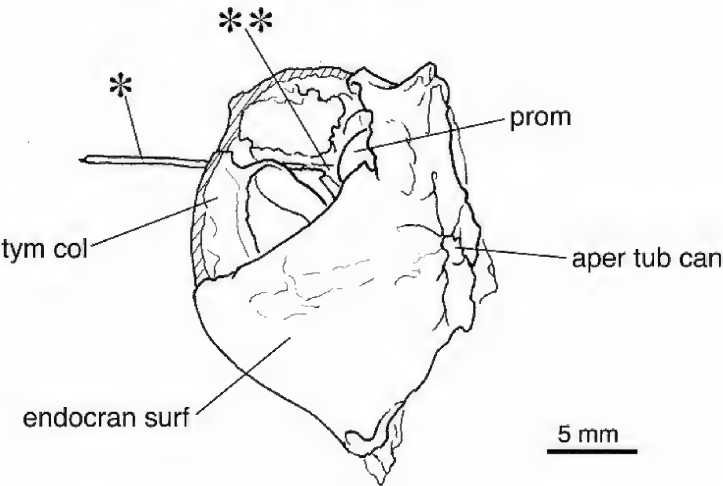
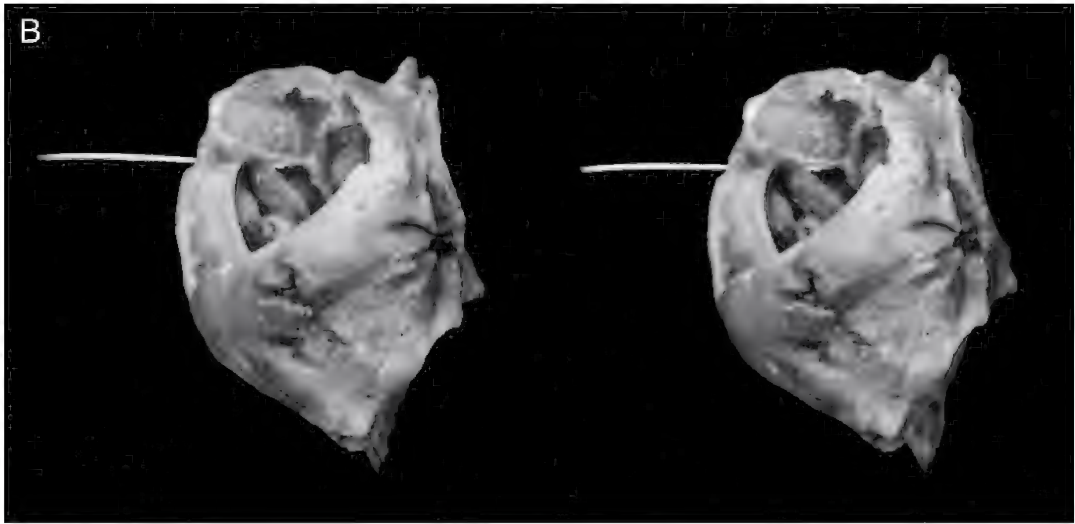


Fig. 19. *Continued.*

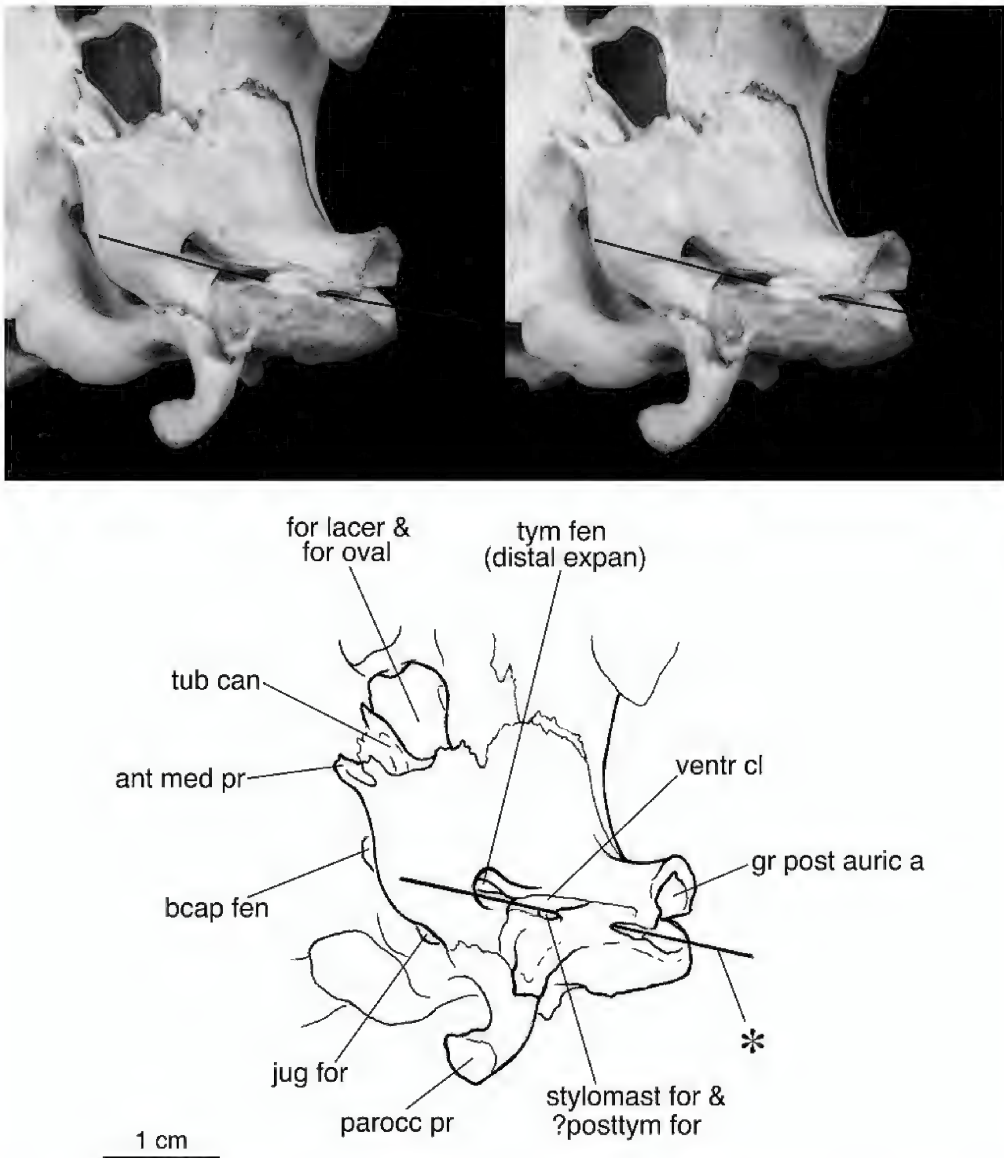


Fig. 20. *Lagostomus maximus* AMNHM 80208, right auditory region (rev.); stereopair view (with key) in ventrolateral aspect. Extensive meatal growth complicates morphological interpretation. The hypertrophied anterior crus actually forms three-quarters of the elongate definitive meatus, with the mastoid region (and even the exoccipital) completing much of the remaining (posterior) wall (see also fig. 25). The relatively unexpanded tip of the posterior crus can still be identified, separating the tympanic fenestra from the stylomastoid foramen. The large aperture distal to the stylomastoid foramen is the entrance to a short canal for the posterior auricular artery (bristle in canal). Next to it is a long trough, incorporating the original site of the mostly obliterated ventral cleft (ectotympano-ectotympanic suture). On the margin of the stylomastoid foramen another medially directed foramen may be found; this is provisionally regarded as the homolog of posttympanic foramen of *Dinomys* (C2:2).

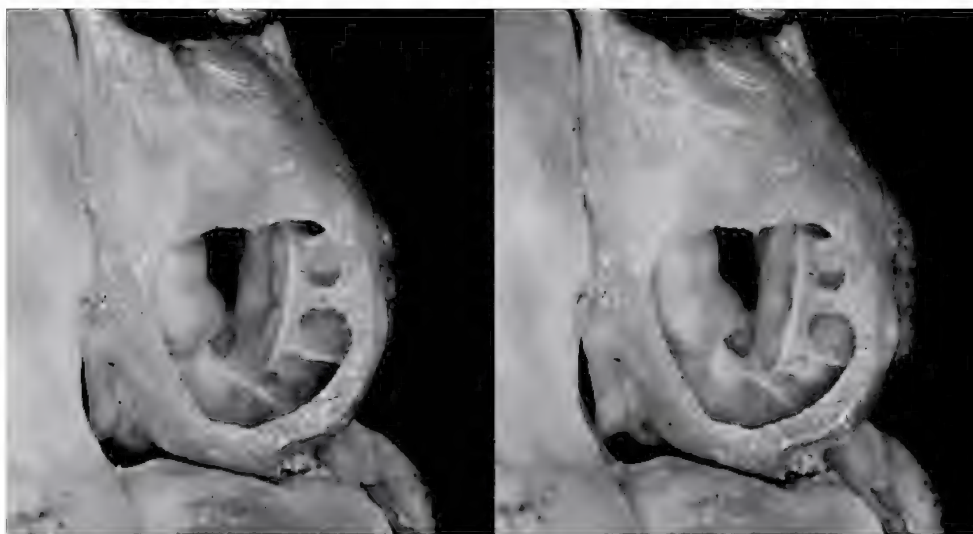


Fig. 21. *Geocapromys brownii* AMNHM 45156, right (rev.) auditory region; stereopair view (with key, opposite page) in ventromedial aspect. Compare with *Elasmodontomys* (figs. 6, 8). Note extreme thickness of bullar wall, which is perforated by thousands of tiny radial channels of unknown significance. A similar microarchitecture occurs in *Echimys* and *Myocastor* (personal obs.), but its incidence in ctenohystricans generally has not been explored.

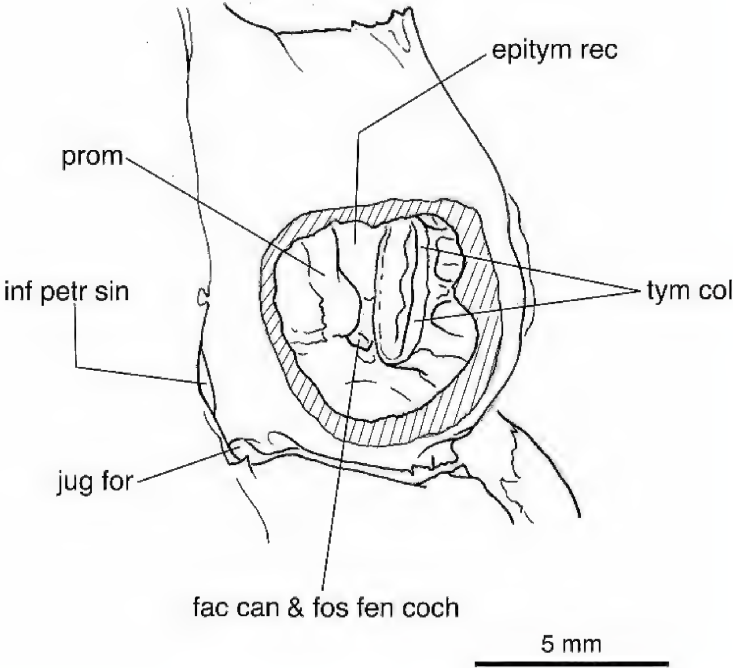


Fig. 21. *Continued.*

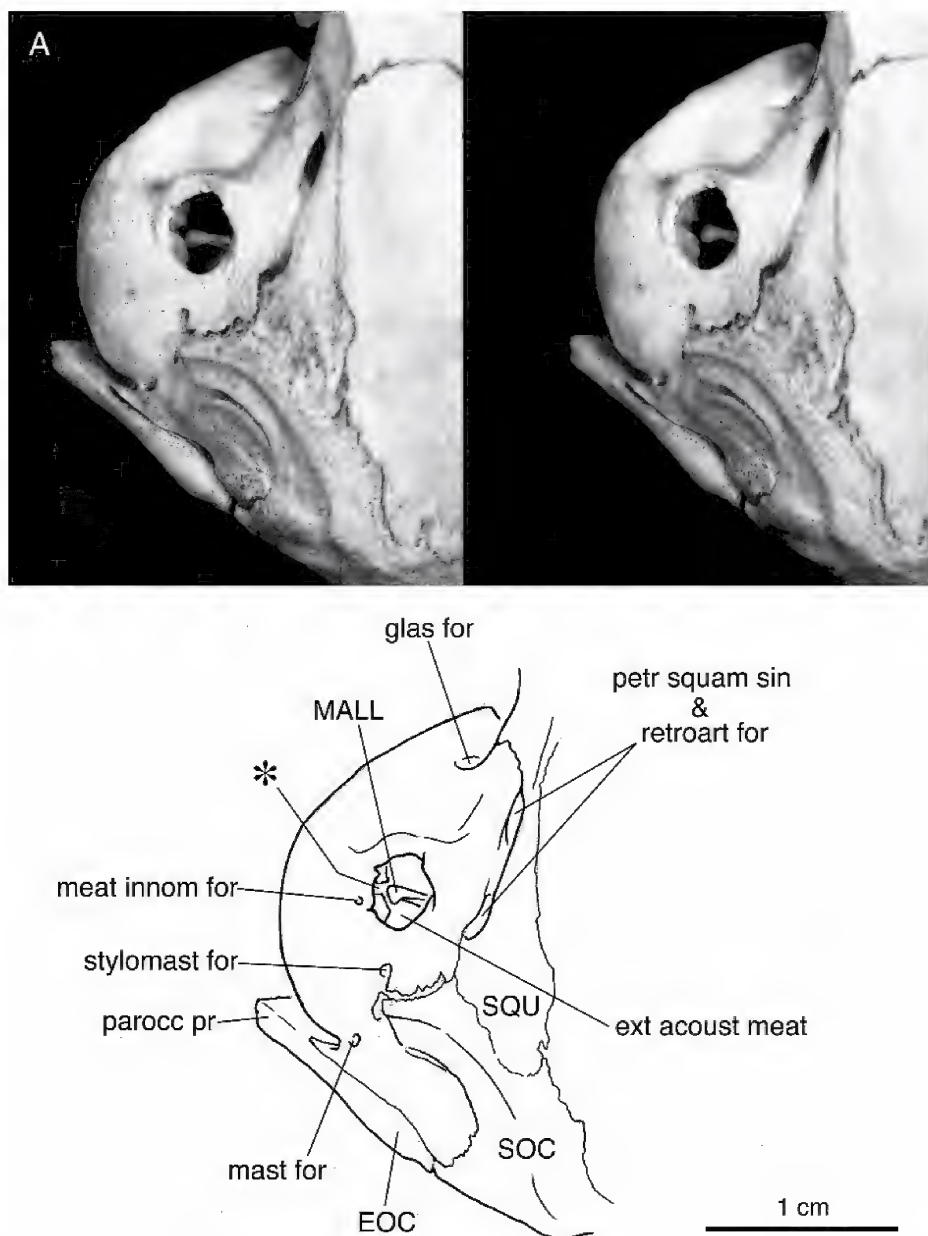


Fig. 22. *Myocastor coypus* AMNHM 80097, right (rev.) auditory region, before (A) and after (B, opposite page) removal of bullar floor; stereopair views (with key) in lateral and posteroventral aspects. In this juvenile nutria, the region of the lateral bullar wall beneath the external acoustic meatus is smooth and unnotched, suggesting that the ectotympanic develops in such a way that a tympanic fenestra is never developed as such. Barely visible in A is a foramen for a large meatal innominate vessel, the track of which scores the floor of the meatus just inside the porus (asterisk). Similar conditions are found in Capromyidae and Echimyidae, close relatives of *Myocastor*. Resemblances extend to middle ear with respect to conformation of cochlea, size of tympanic collar (slightly damaged in this specimen), and details of tympanic roof and epitympanic recess. Asterisk in B: sulcus crossing promontorium (? for tympanic nerve).

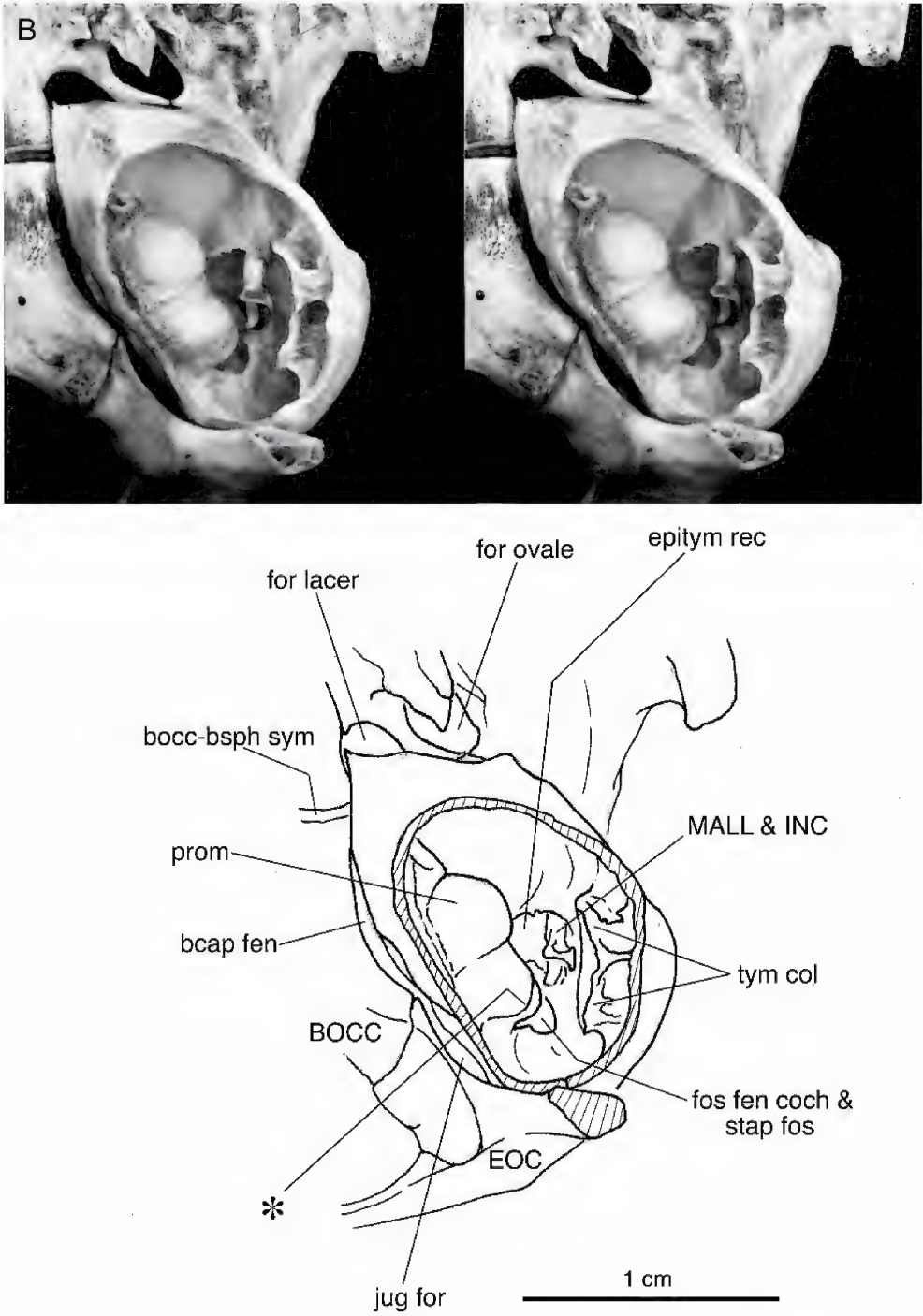


Fig. 22. Continued.

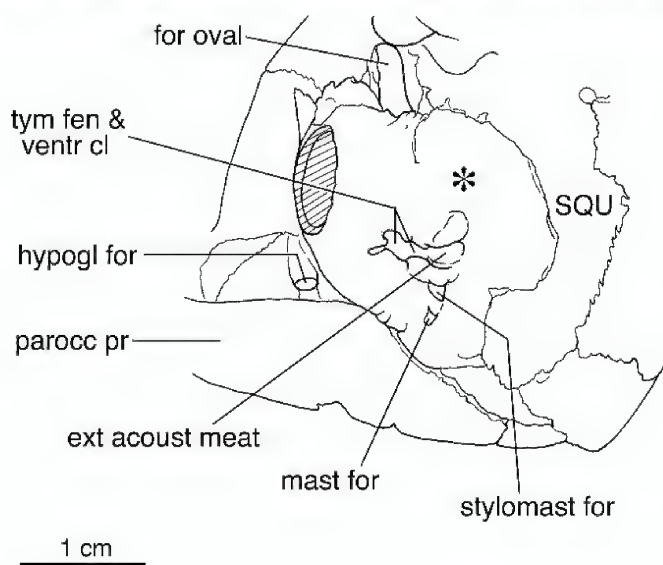
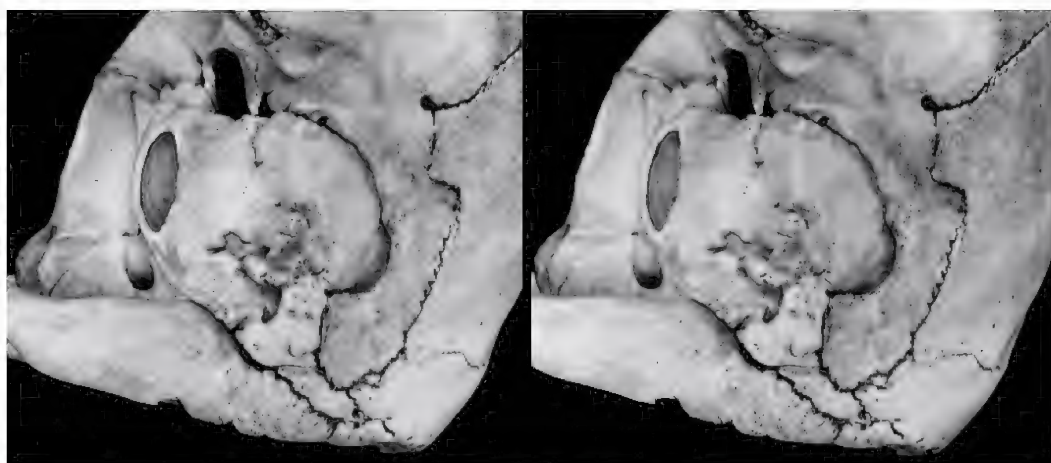


Fig. 23. *Hydrochoerus hydrochaeris* AMNHM 15468, left auditory region of a juvenile specimen; stereopair view (with key) in oblique posterolateral aspect. Ventral floor of bulla partly removed (hatchure); dorsal portion of petrosal, inflated from epitympanic recess, forms prominent bulge externally (asterisk). Note widely communicating tympanic fenestra and external acoustic meatus via patent ventral cleft. In older animals the cleft is relatively narrower, thanks to continued bone growth, but generally remains open.

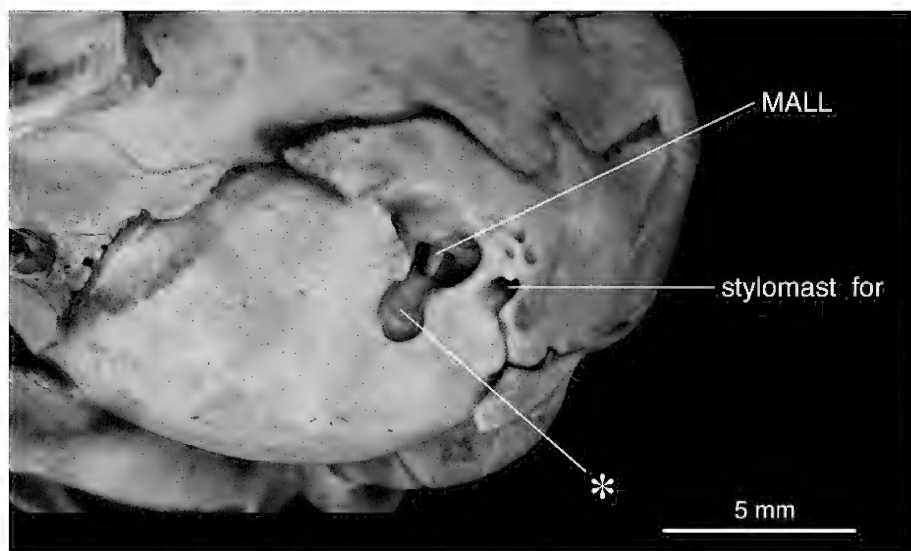


Fig. 24. *Dasyprocta punctata* AMNHM 41394, left auditory region in lateral aspect. Both the notched and bridged conditions are widespread in caviomorphs, and represent different endpoints along the same ontogenetic pathway. In this young specimen the fenestra is widely open and plugged with meatal soft tissues (asterisk) that include, or are derived from, the fibrous membrane of the tympanic cavity (see MacPhee, 1981). Older specimens and adults show the same morphology, indicating that an ectotympano-ectotympanic suture is never formed in this taxon.

developed. In *Myoprocta acouchy* AMNHM 70198 conditions are essentially identical. In this latter specimen the stapedius muscle appears to be completely enclosed in a thin, translucent shell of bone; its tendon travels to the stapes in its own tiny tube. This tube is clearly not a conduit for the ramus post-tympanicus, as it ends as usual on the posterior crus (to which the stapedius tendon normally attaches) and is not directed toward the obturator foramen. The pessulus was absent in the examined specimens of *Dasyprocta*; pessular absence in *Myoprocta acouchy* AMNHM 70198 could not be confirmed but seems probable. A well-developed tympanic fenestra is present in the Deseadan Oligocene species *Incamys bolvianus*, nominally regarded as a dasyproctid (Patterson and Wood, 1982).

Cuniculidae: *Cuniculus paca* AMNHM 2905 and 266567 present conditions similar to those seen in *Dasyprocta* and *Myoprocta* with regard to features of interest, except for absence of the fenestra. As in these taxa, the posterior part of the tympanic cavity is very restricted, with no exterior or interior indication of a ramus posttympanicus. A large foramen near the posterior lip of stylomastoid foramen is directed posteriorly, and is thus a mastoid foramen. The pessulus is absent.

DEVELOPMENT, HOMOLOGY, AND CHARACTER ANALYSIS

TYMPANIC FENESTRA AND DEVELOPMENT OF THE LATERAL BULLAR WALL

Although it would be necessary to have access to developmental series in order to thoroughly document fenestral development in different clades of ctenohystricans, major patterns can be plausibly induced from juvenile and adult conditions, as briefly treated in this section and figure 25. The present investigation indicates that the critical factor in fenestral development is the relative growth rates of the crural margins of the primordial U-shaped ectotympanic. Theoretically, if crural growth rates were roughly similar on both the lateral and the medial aspects of the ectotympanic, the bulla would tend to expand in a simple, balloonlike manner, with the primitive external acoustic meatus appearing

to reduce in relative size as its floor ossifies. Further, if the floor of the meatus were to evenly ossify and remodel in concert with the rest of the lateral bullar wall, as in humans, the fenestra as a "potential space" separate from the meatal aperture should disappear by the definitive stage of development. By contrast, if growth gradients along the crura were such that, for example, one crus tended to preserve its embryonic proportions while the other became greatly expanded, the effect on the meatal floor would be a persistent defect (ventral cleft) in the presumptive margin of the external acoustic meatus. In later ontogeny the defect might remain completely open or partly close, depending on the degree of approximation of bone territories.

Other than the fibrous membrane and associated dense connective tissues, the only structures in the presumptive meatal area are the tympanic membrane and the vascular elements grouped here as meatal innominate vessels. Meatal innominate foramina are common in the target groups, and are found in taxa that exhibit the tympanic fenestra as well as those that do not. It is unlikely that local blood supply has any influence on the relative speed of ossification. Body size is likewise irrelevant to fenestral persistence. Although megafaunal rodents like *Amblyrhiza*, *Eumegamys*, and *Phoberomys* (and perhaps *Josephoartegasia*) all possess a large tympanic fenestra in the adult stage, so do much smaller *Dinomys* and many cavioids. On the other hand, the size of the fenestra is positively correlated with the length of the external acoustic canal, which is itself a proxy for the hyperdevelopment of the anterior crus. This is especially evident in chinchilloids.

The reconstructed ontogeny of the three character states of **C1**, each developing from the indifferent or unexpanded anulus of late fetal life, is depicted in highly diagrammatic form in figure 25. The facial nerve, in its standard or primitive position passing immediately behind the posterior crus (MacPhee, 1981), is provided as a reference point. In order to make character analysis consistent, **C1:0** does not distinguish between complete absence of all apertures in the circummeatal area and presence of one or more meatal innominate foramina. **C1:1** and **C1:2** cover the remaining possibilities, which focus on

whether the fenestra is simply a notch or a separate window, and whether an identifiable ectotympano-ectotympanic suture is formed.

The tympanic floor conformation seen most frequently in mammals is **C1:0** (fig. 25, top), in which the definitive, smoothly rounded meatus is the only sizeable opening in the lateral wall of the bulla. Minor variations on these conditions are seen in many caviomorphs (capromyids, echimyids, and cuniculids) and Old World ctenohystriacans (e.g., *Ctenodactylus gundi* USNMM 325852, fig. 15; *Thryonomys swinderianus* AMNHM 216340, fig. 18). For this pathway the track of a meatal innominate vessel is also shown; it is assumed that such vessels are constantly present, whether or not an evident trackway can be discriminated osteologically.

C1:1 (fig. 25, middle) is possibly a wastebasket grouping, but with the material at hand I am not able to discriminate more than one character state. The recognition criterion for this character state is the *notched* condition of the ventral margin of the meatus. The apex of the notch is either little or not at all expanded, and shapes range from a narrow slit to a triangular gap in the meatal floor.

The only complication in recognizing this character state is that small projections from the margins of the notch may eventually grow together in some taxa or individuals, yielding a *bridged* condition with a large opening above (meatus) and a much smaller aperture below (tympanic fenestra). For example, notches are nearly closed bilaterally in *Dolichotis* sp. AMNHM 48218, an old juvenile, and only just bridged over in *Galea musteloides* AMNHM 213465. In adult *Cavia aspera* AMNHM 264468, bridging is complete, and the distance between fenestra and meatus is very wide indeed. It is not known whether the presence of so-called accessory meatal bones have an effect on fenestral development in this taxon. This last arrangement impinges, at least descriptively, on that described under **C1:2**, although other distinctions also apply. As explained below, the primary difference is that the bony projections of the bridged condition of **C1:1** do not ordinarily form sutural tissues at an early developmental age or lead to the lengthy line of sutural fusion seen in taxa expressing **C1:2**.

Interestingly, some specimens display a notch on one side and a bridge on the other, which points up that these morphologies should be thought of as slightly different outcomes produced along the same general ontogenetic pathway. Thus in the dasyproctid *Dasyprocta punctata* AMNHM 41394, a very young animal in which only the first upper molars are fully erupted, the meatus is deeply notched (fig. 24). This also applies to a somewhat older *D. punctata* AMNHM 23461 (upper third molars erupting), but in the dentally mature *D. punctata* AMNHM 262281 the notch is bridged on the left side and but not on the right.

The hallmark of **C1:2** (fig. 25, bottom) is very marked differential growth of the crura and elongation of the meatus into a long canal, as seen in certain chinchillids (e.g., *Lagostomus maximus* AMNHM 80208, fig. 20). Sutural tissues are inferred to form at an early stage, because in *L. maximus* AMNHM 70222 (47 mm skull length), a juvenile, the ectotympano-ectotympanic suture is already closed, but still detectable. In the adult stage, a low ridge or seam may be seen running along the line of fusion inside the meatus, marking the line of contact (see *Amblyrhiza inudata* AMNHVP 11842; fig. 5). *Chinchilla* is essentially the same as *Lagostomus*, except that pneumatization is so pronounced in this genus that the original form of the crura is entirely masked. However, the closed ventral cleft can easily be distinguished on the lateral bullar wall.

In summary (see also fig. 27), there are no morphological grounds at present for inferring that the fenestra develops, and later disappears, during the ontogeny of most phiomorphs. (*Petromus* is the only extant contrary example, although this point should be checked in fossil taxa.) Within Caviomorpha, at the superfamily level the fenestra is absent in adult erethizontoids (i.e., inferior margin never notched, meatal innominate vessels small). In adult stages of extant octodontoids the fenestra is either absent or no more than a small aperture, in many cases bridged off from the meatus by a strap of bone. In most taxa that express a definite fenestra, margins remain rather ragged, as might be expected in an imperfectly ossified region. However, in others the aperture is

small and rounded, and functions exclusively as a true foramen for transmitting vasculature (e.g., *Spalacopus cyaneus* AMNHM 33276; *Myocastor coypus* AMNHM 35626). In cavioids and chinchilloids, by contrast, the fenestra is usually fairly large relative to the size of the external acoustic meatus.

Amblyrhiza agrees more closely with conditions in *Lagostomus* and other chinchillids than with *Dinomys*, in that it possesses a markedly elongated external acoustic canal and a fused ectotympano-ectotympanic suture in the adult in combination with a patent tympanic fenestra. The skull of *Eumegamys*, although damaged in the critical area, agrees closely with *Dinomys* in retaining an open ventral cleft and much shorter external acoustic canal. *Elasmodontomys* resembles the majority of octodontoids in completely lacking a fenestra.

RAMUS POSTTYMPANICUS AS STAPEDIAL RAMUS POSTERIOR

Is the occupant of the posttympanic canal found in some caviomorphs in fact the homolog of the stapedial ramus posterior, a vessel never previously identified in a rodent? From a comparative standpoint, this question is not as unlikely as it may seem. In several basicranially primitive placental taxa (*Erinaceus*, *Solenodon*, and several tenrecs) that preserve an intact, primitive stapedial system, the ramus posterior is a branch released by the parent vessel just before the latter passes through the obturator foramen of the stapes (MacPhee, 1981). In *Erinaceus* the ramus posterior is very small, supplies only the area of the stapedius fossa, and evidently involutes in early postnatal life. In tenrecs and, especially, *Solenodon*, it is a large vessel that travels outside the confines of the middle ear in close relation to the facial nerve (MacPhee, 1981). Recently, Wible (2008) confirmed that the ramus posterior in *Solenodon* supplies the area conventionally associated with the posterior auricular artery in other mammals (pinna and related structures in the rear part of the head).

In *Homo*, a vessel with somewhat similar relations, but lacking its own foramen and individual bony conduit, is the stylomastoid branch of the posterior auricular artery.

Whether this vessel may itself be a stapedial remnant has never been properly discussed in the general morphological literature, let alone that oriented toward Rodentia. Thus, Aihara (1958) noted that a branch of the stylomastoid artery—his “stapedial artery”—feeds the stapedial muscle in *Cavia*. However, he did not consider whether both, either, or neither might be homologous with any part of the primitive stapedial system. As *Cavia* definitely lacks a posttympanic canal (see below), the situation remains as ambiguous in this taxon as in any other.

While the possible equivalency of the ramus posttympanicus and part or all of the stylomastoid artery's distributary network is worth acknowledging, there are other observations that suggest a different picture for hystricognaths. Although Wible (1984) did not encounter a ramus posterior in any of the taxa he personally examined for his monumental study of mammalian cephalic arterial systems, in his literature review he noted some additional instances of the probable or possible occurrence of this vessel. One such instance is directly relevant here: Struthers' (1930) study of cephalic arterial development in fetal *Erethizon*, in which this author described an “occipital” artery transitorily linked to the developing proximal stapedial. Wible (1984) commented that the stapedial “occipital” connection traveled in close relation to the facial nerve and stapedius muscle, just as in verified occurrences of the ramus posterior in nonhystricognaths. Whether the porcupine “occipital” is homologous with the posterior auricular of *Homo* cannot be determined from the information provided by Struthers, but that is certainly a possibility.

The question that immediately occurs is whether the arrangement seen in fetal erethizontids can be generalized to explain some of the findings presented in this paper. Figure 26 illustrates a possible, although speculative, interpretation. In some unspecified caviomorph (or hystricognath) ancestor the entire primitive stapedial system is inferred to have been present (fig. 26A), fed by the internal carotid stem, and perhaps largely functional in the adult. The ramus posterior might have already possessed the indicated connection with the posterior auricular, or this may have developed later on when the

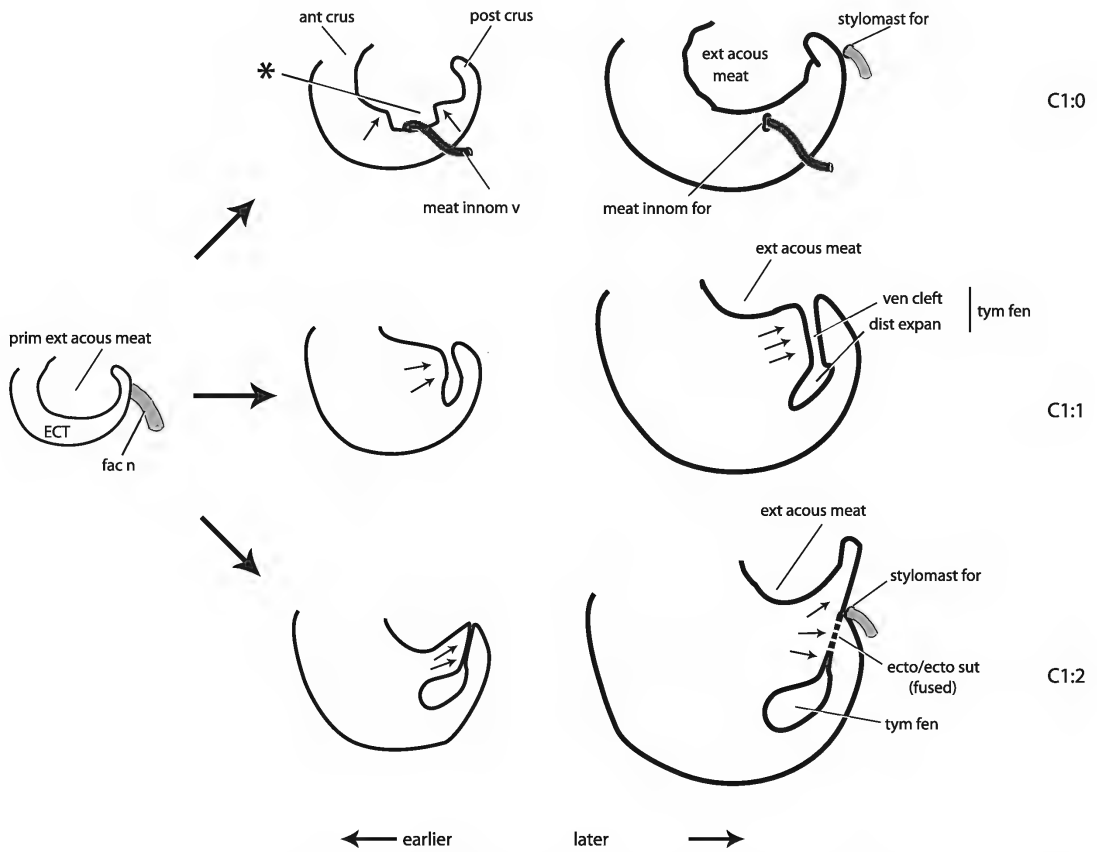


Fig. 25. Development of the tympanic fenestra: inferred ontogenetic pathways for patterns culminating in C1:0, C1:1, and C1:2 (top to bottom, then left to right). Cartoons are highly diagrammatic. Small arrows figuratively suggest major growth directions along meatal margin. Indifferent (youngest) stage, shown as primitive for all three character states, is based on known aspects of ectotympanic development in mammals (MacPhee, 1981). Intermediate and advanced stages partly based on these specimens: C1:0, *Myocastor coypus* AMNHM 80097, *Bathyergus* sp. AMNHM 168284; C1:1, *Dasyprocta punctata* AMNHM 41394, *Hydrochoerus hydrochaeris* AMNHM 98631; C1:2, *Lagostomus maximus* AMNHM 70222, *Lagidium viscacia* AMNHM 38981. For character state distribution in extant ctenohystricans, see appendix 2. In C1:0 (fenestra absent), ventral meatal margin (asterisk) may ossify more slowly than surrounding areas, but a proper tympanic fenestra is not normally present in adult. However, meatal innominate vessels may become enclosed where they cross the ossification front, leading to the definition of one or more small foramina. In C1:1 (tympanic fenestra present as a notch), the region of the bullar wall ventral to the presumptive meatus remains persistently unossified, leaving a narrow, distally expanded cleft. The cleft may stay in permanent communication with the true meatus, or a small tab of bone may grow out from one of the meatal borders and close it off (bridged condition). Fusion may follow, but occurs late in development. In C1:2 (tympanic fenestra isolated from meatus by suture), the anterior crus and body of the ectotympanic grow at a much faster pace than the posterior crus. Contact between the tips of the two crura occurs early, forming a true (ectotympano-ectotympanic) suture that separates the presumptive tympanic fenestra from the porus meatus. Meatus is typically greatly elongated in taxa displaying this pathway; at least in *Lagostomus* and close relatives, the anterior crus extends posteriorly to press against the mastoid region. Suture normally fused by late fetal or juvenile stage.

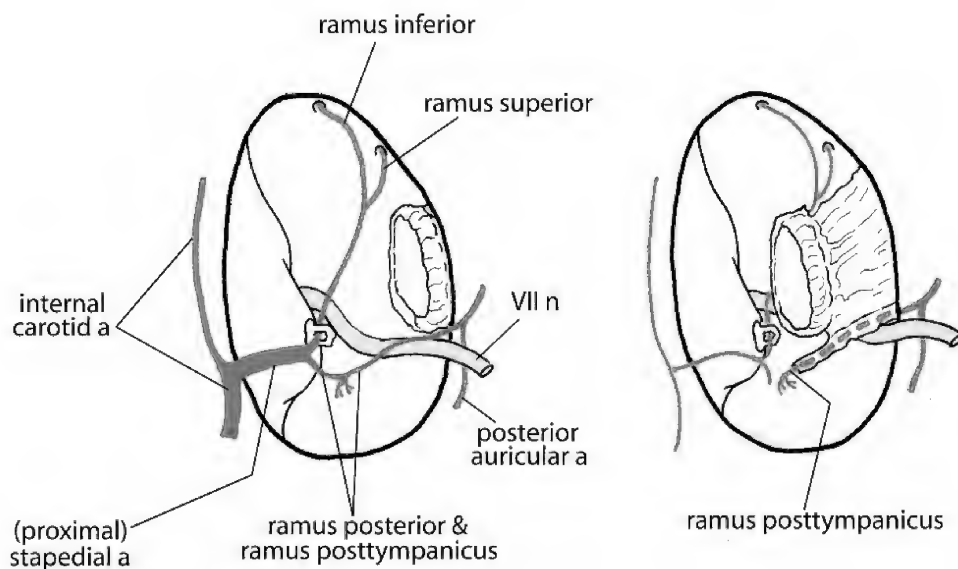


Fig. 26. Theoretical interpretation of developmental interconnections among internal carotid, stapedial, and posterior auricular arteries in the ctenohystrican Bauplan, based on evidence discussed in the text. All diagrams are idealized for interpretative purposes; actual ontogeny is unknown. **A**, Hypothetical, fully elaborated arrangement, with proximally intact, medially positioned internal carotid providing blood to stapedial system exhibiting all three rami. Note anastomotic link or continuity between ramus posterior and posterior auricular via ramus posttympanicus. Note also small distributaries to stapedius muscle, inferred to be ramus inferior's primitive area of supply on basis of conditions in several tenrecs and eulipotyphlans *Erinaceus* and *Solenodon* (MacPhee, 1981). Whether, and to what degree, this arrangement is primitive for placentals more generally is not known. **B**, Example of a derived arterial arrangement, partly based on conditions in *Amblyrhiza*. For this taxon there is firm evidence only for the presence of the ramus posttympanicus; other parts of the internal carotid/stapedial system may have completely involuted by adult stage, or never formed. Blood supply to ramus posttympanicus here interpreted to have been retrograde, from posterior auricular. Pattern also applies to *Dinomys*, but may be inferred for *Eumegamys* and possibly certain other caviomorphs (including chinchillids and erethizontids).

stapedial system as a whole began to involute. With involution, the distalmost segment—now as the ramus posttympanicus—would have crossed the track of the facial nerve and continued to supply the area of the stapedius fossa, possibly via retrograde blood flow from its anastomotic partner as suggested in figure 26B (which purposely mimics conditions in *Amblyrhiza*, although apart from the ramus posttympanicus there is no conclusive evidence for other possible stapedial vestiges in this taxon). How much of the resultant arterial pathway should be considered equivalent to the original ramus posterior and how much to the neomorphic anastomosis is impossible to say without more evidence. The best course would be to

retain the name “ramus posttympanicus” for the whole structure, even though it may well incorporate material ultimately derived from more than one primitive source.

There are other clues that a vestigial stapedial network still exists in extant caviomorphs. One is the inferior tympanic artery identified in *Cavia* by Aihara (1958), which has some of the characteristics one would expect to find in a vestige of the primitive stapedial stem: it exhibits anastomotic links with both the middle meningeal and the vessel issuing from the stylomastoid artery that Aihara (1958) confusingly named “the” stapedial artery (see above). Another is the “ramus tympanicus” of the maxillary artery that provides a “supply to the middle ear” in

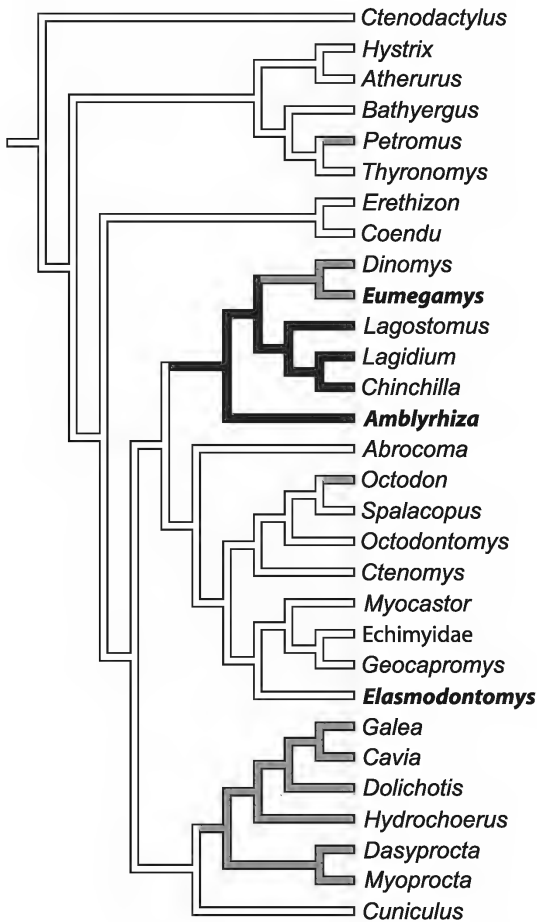


Fig. 27. Character trace for **Character 1: Absence/presence of tympanic fenestra** (0, white; 1, grey; 2, black). With this topology, **C1:2, isolated, suture-delimited aperture** emerges as a diagnostic feature of extant Chinchillidae + *Amblyrhiza*, with no examples of convergence and with *Dinomys* and *Eumegamys* showing an alternative state. Placing *Amblyrhiza* among octodontoids as a relative of *Geocapromys*, as some authors have suggested, seems unparsimonious in light of the fact that in this superfamily neither this state nor (with the exception of *Octodon*) the less derived state, **C1:1, notch only (bridged or unbridged)**, is known to occur. In this and the following figure “Echimyidae” refers to the four representative taxa of spiny rats selected for study (*Echimys*, *Proechimys*, *Lonchothrix*, *Dactylomys*), which are invariant for the characters traced.

Cavia according to Cooper and Schiller (1975: 151). Its position of origin seems too rostral for it to represent one of the meatal innominate vessels of this paper. Although there are several plausible homologies, it is possible that the “ramus tympanicus” may be yet another remnant of the stapedia system (?ramus inferior)—in this case, one that has been pirated by the maxillary and which now delivers retrograde flow to some part of the tympanic cavity (for parallel cases in primates, see Diamond, 1991). Another is the apparent retention of a foramen of exit for the ramus superior (evidently maintained for meningeal supply) on the cerebral side of the petrosal in *Lagostomus* (cf. Bugge’s [1974b: fig. 6D] illustration of an injected specimen). It would be of great interest to know whether the vessel traversing this foramen anastomosed with the ramus posttympanicus or with the stylomastoid artery (assuming these are different entities in the plains viscacha).

Also possibly relevant is Tandler’s (1901: 360) alleged detection of a highly reduced internal carotid artery in *Hystrix*: in his interpretation, the vessel entered the middle ear through a tiny aperture on the posterior side of the bulla, then traveled in a groove transpromontorially in company with the internal carotid nerve toward the cranial cavity. Dierbach (1985) found a “carotid foramen,” but no artery traversing it, in a 25 mm CRL fetus of *Cavia*; from this indirect (and admittedly inadequate) evidence he inferred that the internal carotid artery was formed but had already involuted. Although carotid involution occurs during the ontogeny of many placentals, loss need not be complete and some structures may be retained as functionless or near-functionless remnants (Bugge, 1974b; MacPhee, 1981; Wible, 1984; Diamond, 1991). Cooper and Schiller (1975: fig. 4–15) claim that a highly reduced version of this artery exists in adult *Cavia*, but this has not been confirmed either. Indeed, whether any nonerethizontid ctenohystrican possesses an intact internal carotid artery at any stage of development remains to be properly demonstrated. By contrast, a much more credible case can be made for the persistence and repurposing of parts of the primitive stapedia system.

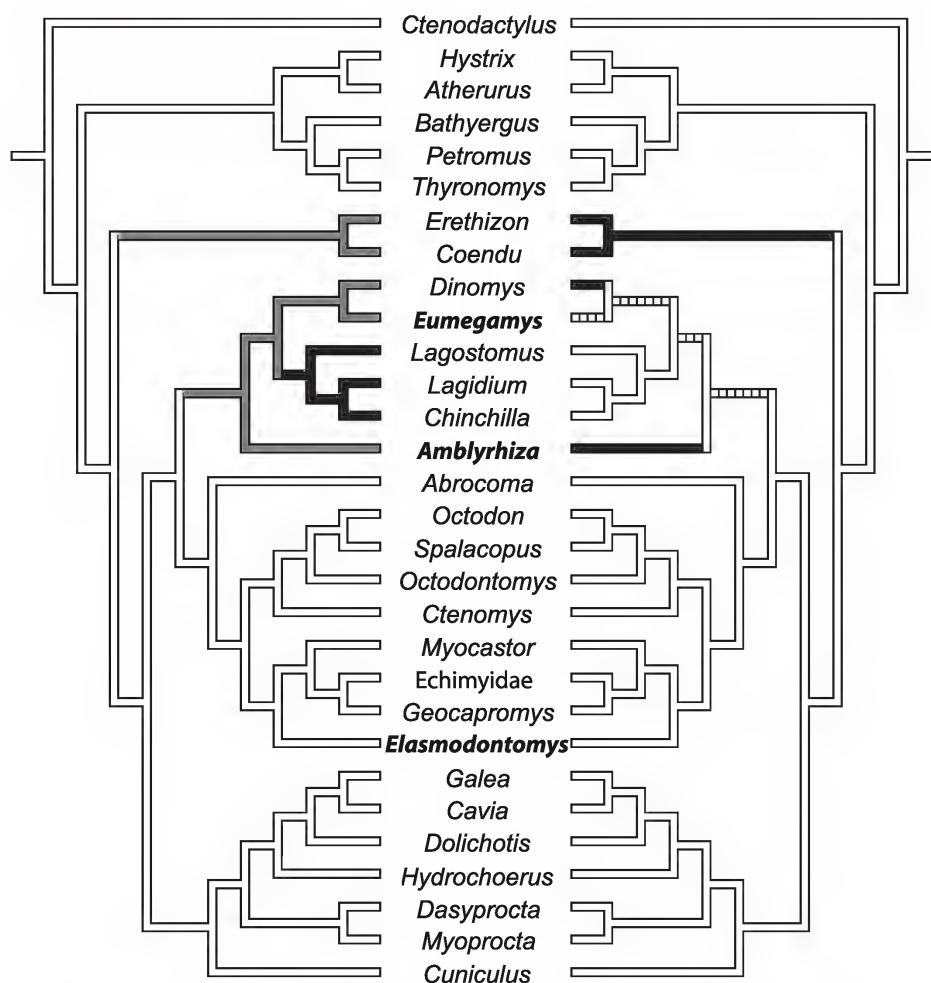


Fig. 28. Character traces for, on left, **Character 2: Absence/presence of posttympanic foramen** (0, white; 1, grey; 2, black; vertical striping, equivocality), and, on right, **Character 3: Absence/presence of posttympanic canal** (0, white; 1, black; vertical striping, equivocality). “Canal present” implies a visible, distinguishable structure. These characters are difficult to score in the absence of adequate comparative documentation on basicranial vasculature in ctenohystricans. In any case, the posttympanic foramen/canal complex (**C2:1/ C2:2 + C3:1**) broadly characterizes erethizontoids and chinchilloids but no other ctenohystricans, as far as is now known. The topology utilized in the diagrams favors the conclusion that the complex is a convergence between New World porcupines and chinchillas and their relatives. However, if the ramus posttympanicus is in fact related to the ramus posterior of the placental morphotype, then the resemblances are either primitive retentions or the result of de novo reacquisitions.

SYSTEMATIC SIGNIFICANCE

Despite a certain amount of recent attention, a number of aspects of ctenohystrican phylogeny are still not well resolved (e.g., superfamilial and major-clade relationships within Caviomorpha). In light of this, tracing character distributions on a plausible composite tree is likely to be of more use at

present than “testing” systematic hypotheses with tiny character sets. The overall tree topology used in figures 27–29 to present character optimizations ultimately derives from Huchon and Douzery’s (2001) study, with familial and other downtree relationships reflecting more recent analyses (Rowe and Honeycutt, 2002; Spotorno et al., 2004; Galewski et al., 2005; Morgan, 2009). I have

2. **Relationships of *Elasmodontomys*.** This genus is nondescript basicranially, resembling a wide variety of other taxa—but not *Amblyrhiza* in particular or chinchilloids in general. It is thus of some interest to note that, in their study, Woods and Hermanson (1985: 533) concluded that *Elasmodontomys* “groups most closely with *Myocastor coypus* and is not very distinct from capromyids. *Elasmodontomys* stands clearly apart from *Dinomys*, with which it has been grouped by some authors in the past.... We propose placing the [Antillean] heptaxodontids within the superfamily Octodontoidea, based on the elongated acromion process of *Elasmodontomys*, and would associate this family adjacent to the West Indian Family Capromyidae with which it may share a common evolutionary history.” Woods and Hermanson (1985) did not have evidence of acromial morphology in any of the other Antillean heptaxodontids, but evidently assumed that they would be similar. In the epigraph at the head of this paper, Woods (1982) admits that his “Capromyidae-Heptaxodontidae clade” is exceedingly diverse, but that is only true if the classic organization of Antillean heptaxodontids is retained. Breaking out *Elasmodontomys* changes things dramatically. There is nothing in the auditory regions of *Elasmodontomys*, *Myocastor*, and capromyids/echimyids—notably, if plesiomorphously, similar—which would preclude their close phylogenetic association, despite the assertion of Patterson and Wood (1982: 512) that *Elasmodontomys* cannot be closely related to echimyids because it replaced its deciduous premolars. If the acromial evidence is correctly interpreted to mean that *Elasmodontomys* is an octodontoid, then any dental resemblances to chinchilloids are spurious. On the other hand, according to Martin (1992), octodontoids are unified by their incisor enamel pattern (*Schmeltzmuster*), which features low-angle interprismatic matrix not seen in either *Amblyrhiza* or *Elasmodontomys* (which show instead the plesiomorphic, acute-angle character

state): While this observation is pertinent, the seating of the Puerto Rican rodent remains quite uncertain at this time, and in the tree diagram I prefer to place *Elasmodontomys* next to *Myocastor* and capromyids/echimyids without specifying which, if either, is its sister taxon.

3. **Current Status of the Problem of Antillean Heptaxodontidae.** As noted in the Introduction, the “problem” may be said to have originated with Anthony’s (1917: 186) proposal that, because the “identical tooth structure” of platetooth rodents could not have been due to convergence, then these taxa must in fact be closely related. In fact, the teeth of *Amblyrhiza*, *Elasmodontomys*, and *Clidomys* are far from identical (see Pascual et al., 1990). Given the limited specialist interest in the group, it is unsurprising that most commentators have been content to simply leave “Antillean Heptaxodontidae” as is, or place an asterisk beside the name to imply possible paraphyly (e.g., MacPhee and Flemming, 2003). The issue is now partly resolved, at least to the extent that basicranial evidence does not support a close relationship between the central taxa *Amblyrhiza* and *Elasmodontomys*.

Heptaxodontinae remains the appropriate subfamily name for any monophyletic group containing *Elasmodontomys obliquus* (= *Heptaxodon bidens*) (Ray, 1964, 1965). Although *Amblyrhiza* can no longer be considered to be a member of such a group, what about the other nominal Antillean heptaxodontids? *Quemisia*, known only from a few isolated teeth, a jaw, and a partial femur, is arguably the most *Elasmodontomys*-like (or echimyid/capromyid-like) of the remaining taxa, as pointed out in detail by Ray (1964, 1965). So is *Tainotherium*; in fact, the holotype femur so strongly resembles that of *Elasmodontomys* that here we may have a distinction without a difference (Bover and MacPhee, 2007). *Clidomys* remains a puzzle; while there are scattered resemblances to *Amblyrhiza* (Morgan and Wilkins, 2003), dentally *Clidomys* is as much, or more, like neoepiblemids (at least as defined by Pascual et al., 1990),

suggesting that there might have been one more invasion of the Greater Antilles by a large-bodied caviomorph group than is usually counted. *Xaymaca* is the most obscure of all: MacPhee and Flemming (2003) made strenuous efforts to show that it might be a diminutive heptaxodontid, but a more realistic positioning for the seriously incomplete holotype of this taxon may be simply Caviomorpha, incertae sedis. This is as far as things can be reasonably taken at present. A more comprehensive answer will have to await analyses of other understudied character sources (e.g., tarsals, other postcranials; MacPhee, 1984; Horovitz et al., 2006), not only with reference to the insular forms discussed here, but also to the confused tangle of continental South American taxa that have been sometimes regarded as “heptaxodontids.”

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a self-described psychedelic/electronic music group from Utrecht, Netherlands (<http://www.myspace.com/amblyrhiza>).

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APPENDIX 1
Specimens of Extant Species Examined for This Study

Family/Genus	Species	Accession No. ^a	Stage ^b	Sex ^c
Ctenodactylidae				
<i>Ctenodactylus</i>	<i>gundi</i>	325852*	A	?
<i>Ctenodactylus</i>	<i>gundi</i>	325857*	A	?
Hystriichidae				
<i>Hystrix</i>	<i>indica</i>	88701	A	?
<i>Hystrix</i>	sp.	240917	A	M
<i>Hystrix</i>	<i>africae</i>	216336	A	M
<i>Atherurus</i>	<i>macrourus</i>	60045	A	?
<i>Atherurus</i>	<i>macrourus</i>	87586	A	M
Bathyergidae				
<i>Bathyergus</i>	sp.	168284	A	F
<i>Bathyergus</i>	sp.	168287	A	M
Petromuridae				
<i>Petromus</i>	<i>typicus</i>	165295	A	M
<i>Petromus</i>	<i>typicus</i>	34393	A	?
<i>Petromus</i>	<i>typicus</i>	165296	A	M
<i>Petromus</i>	<i>typicus</i>	89051	A	M
Thryonomyidae				
<i>Thryonomys</i>	<i>swinderianus</i>	54000	A	M
<i>Thryonomys</i>	<i>swinderianus</i>	216340	A	M
Erethizontidae				
<i>Erethizon</i>	<i>dorsatum</i>	1211197	A	?
<i>Erethizon</i>	<i>dorsatum</i>	20773	A	?
<i>Coendu</i>	<i>mexicanus</i>	204282	J	F
Dinomyidae				
<i>Dinomys</i>	<i>branickii</i>	70354	A	?
<i>Dinomys</i>	<i>branickii</i>	185372	A	?
<i>Dinomys</i>	<i>branickii</i>	46551	A	F
Chinchillidae				
<i>Chinchilla</i>	<i>laniger</i>	254506	A	?
<i>Lagostomus</i>	<i>maximus</i>	70222	J	M
<i>Lagostomus</i>	<i>maximus</i>	246958	A	F
<i>Lagostomus</i>	<i>maximus</i>	214770	A	?
<i>Lagostomus</i>	<i>maximus</i>	80208	A	?
<i>Lagidium</i>	<i>peruanum</i>	91670	A	F
<i>Lagidium</i>	<i>viscacia</i>	38981	J	F
<i>Lagidium</i>	sp.	144954	A	?
Abrocomidae				
<i>Abrocoma</i>	<i>bennettii</i>	33273	A	M
Octodontidae				
<i>Octodon</i>	<i>degus</i>	242476	A	M
<i>Octodontomys</i>	<i>gliroides</i>	249052	A	M
<i>Spalacopus</i>	<i>cyanus</i>	33276	A	M
Ctenomyidae				
<i>Ctenomys</i>	<i>colburni</i>	25673	A	M
<i>Ctenomys</i>	<i>conoveri</i>	262290	A	F
<i>Ctenomys</i>	<i>lewisi</i>	264543	A	F

APPENDIX 1
(Continued)

Family/Genus	Species	Accession No. ^a	Stage ^b	Sex ^c
<i>Ctenomys</i>	<i>magellanicus</i>	17445	A	?
Myocastoridae				
<i>Mycastor</i>	<i>coypus</i>	35626	A	M
<i>Mycastor</i>	<i>coypus</i>	80097	J	?
Echimyidae				
<i>Echimyys</i>	sp.	97325	A	?
<i>Proechimys</i>	<i>guyannensis</i>	94851	A	F
<i>Proechimys</i>	<i>guyannensis</i>	37485	J	F
<i>Lonchothrix</i>	<i>emiliae</i>	95568	J	F
<i>Dactylomys</i>	<i>dactylinus</i>	92952	A	F
<i>Dactylomys</i>	<i>dactylinus</i>	94045	J	M
Capromyidae				
<i>Geocapromys</i>	<i>brownii</i>	45157	A	M
<i>Geocapromys</i>	<i>brownii</i>	45156	A	M
Caviidae				
<i>Cavia</i>	<i>aperea</i>	264468	A	M
<i>Galea</i>	<i>musteloidea</i>	213465	A	M
<i>Dolichotis</i>	<i>patagonum</i>	48218	A	?
<i>Dolichotis</i>	<i>patagonum</i>	80123	A	F
<i>Hydrochoerus</i>	<i>hydrochaeris</i>	15468	J	?
<i>Hydrochoerus</i>	<i>hydrochaeris</i>	98631	J	M
<i>Hydrochoerus</i>	<i>hydrochaeris</i>	206444	A	?
<i>Hydrochoerus</i>	<i>hydrochaeris</i>	98634	A	?
<i>Hydrochoerus</i>	<i>hydrochaeris</i>	134102	A	?
Dasyproctidae				
<i>Dasyprocta</i>	<i>punctata</i>	23461	A	M
<i>Dasyprocta</i>	<i>punctata</i>	262281	A	?
<i>Dasyprocta</i>	<i>punctata</i>	61440	A	M
<i>Dasyprocta</i>	<i>punctata</i>	41394	J	F
<i>Myoprocta</i>	<i>acouchy</i>	70198	A	M
<i>Myoprocta</i>	<i>acouchy</i>	35625	A	M
Agoutidae (Cuniculidae)				
<i>Cuniculus</i>	<i>paca</i>	266567	J	M
<i>Cuniculus</i>	<i>paca</i>	29605	A	M

^aUSNM specimens marked with asterisk; all others, from AMNHM collection.

^bA, adult; J, juvenile (as determined from dental and suture closure evidence).

^cF, female; M, male; ?, unknown or unrecorded.

APPENDIX 2
DATA MATRIX^a

Taxon	Characters			
	C1	C2	C3	C4
<i>Ctenodactylus gundi</i>	0	0	0	1
<i>Hystrix africae</i>	0	0	0	0
<i>Atherurus macrourus</i>	0	0	0	0
<i>Bathyergus</i> sp.	0	0	0	0
<i>Petromus typicus</i>	1	0	0	1
<i>Thyromys swinderianus</i>	0	0	0	0
<i>Erethizon dorsatum</i>	0	1	1	0
<i>Coendu mexicanus</i>	0	1	1	0
<i>Dinomys branickii</i>	1	1	1	0
<i>Eumegamys paranensis</i>	1	1	?	?
<i>Amblyrhiza inundata</i>	2	1	1	?
<i>Lagostomus maximus</i>	2	2	0	1
<i>Lagidium viscacia</i>	2	2	0	1
<i>Chinchilla laniger</i>	2	2	0	1
<i>Abrocoma bennettii</i>	0	0	0	1
<i>Octodon degus</i>	1	0	0	1
<i>Spalacopus cyanus</i>	0	0	0	0
<i>Octodontomys gliroides</i>	0	0	0	1
<i>Ctenomys magellanicus</i>	0	0	0	1
<i>Myocastor coypus</i>	0	?	0	1
<i>Echimys</i> sp.	0	0	0	0
<i>Dactylomys dactylinus</i>	0	0	0	0
<i>Lonchothrix emiliae</i>	0	0	0	0
<i>Proechimys guyannensis</i>	0	0	0	0
<i>Geocapromys brownii</i>	0	0	0	1
<i>Elasmodontomys obliquus</i>	0	0	0	?
<i>Galea musteloidea</i>	1	0	0	1
<i>Cavia aperea</i>	1	0	0	1
<i>Dolichotis patagonum</i>	1	0	0	1
<i>Hydrochoerus hydrochaeris</i>	1	0	0	0
<i>Dasyprocta punctata</i>	1	0	0	0
<i>Myoprocta acouchy</i>	1	0	0	?
<i>Cuniculus paca</i>	0	0	0	0

^aFor character and character state definitions and scoring, see table 2; “?”= missing data.